

**The social organisation and behaviour of dolphins
(*Tursiops aduncus*) and baboons (*Papio ursinus*):
some comparisons and assessments**

by

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INTRODUCTION

The ecological and behavioural study of free-ranging monkeys and apes formed one of the most rapidly expanding fields of biological research in the last decade (Altmann, 1967). Of no less importance for comparative psychobiology was the increase in systematic studies of the smaller cetaceans, the group of large-brained marine mammals including dolphins and pilot whales. It has been stated that there are several striking similarities in the social behaviour of some of the higher primates and dolphins (Morgan, 1968)—two forms occupying very different environments and differing markedly in anatomical and morphological characteristics—but few comparative studies of dolphins have been published since that of McBride and Hebb (1948). This may be due to the practical difficulties in obtaining good quantitative data on dolphins in the wild.

Indeed, reviewing the field of communication in marine mammals, Evans and Bastian (1969) were impressed by the dearth of knowledge of the social life and ecology of the cetaceans. They write: "We urgently require ethological work on individual species and comparative behavioral studies, not only for the sake of advancing our understanding of social communication in these groups, but also for the light these studies may shed on the many shadowy portions of their systematics that now exist. In many ways, the current state of this field of research is very reminiscent of the recent history of primate behavior studies. Popular interest has long supported public display of captive primates in much the same way that the cetacean and pinniped displays now enjoy the public's fancy. But although much was written about primate social behavior based on the close observation of these captive groups, a large part of the ideas that resulted from these efforts has been forced to be drastically revised. The recent flourishing of ecologically sophisticated studies of free-ranging populations that has been the happy lot of behavioral primatology has provided a much deeper and fuller understanding of the social life of these animals than had been previously thought possible. Our fervent hope is that the same history will unfold in the study of the social behavior of marine mammals." (Evans and Bastian, 1969, pp. 470—1).

It is not only great practical difficulties, however, that hampers the study of free-ranging dolphins, but also that the cetaceans lack the relatively familiar facial expressions and the diversity of the communicative behavioural postures of the higher primates. Visual perception and signal movements appear to be of less importance to dolphins than to primates. Vision, particularly in the faster swimming varieties of dolphins frequenting murky water, is at best reduced to a few metres and therefore a sophisticated system of acoustical echolocation, communication and social co-ordination has evolved (Kellogg, 1959; Lilly, 1961). Although behaviour and the system of communication in captive dolphins have been intensively studied at the Port Elizabeth Oceanarium for seven years (Tietz and Tayler, 1964) little has as yet been reported on the social behaviour of free-ranging dolphins in the Indian Ocean. Comparisons

have frequently been drawn between the behaviour and intelligence of dolphins and of man; whereas the tendency to anthropomorphise should be guarded against, as Caldwell and Caldwell (1968a) have stressed, comparisons between dolphins and terrestrial mammals are valuable for the insights they may provide. The baboons are one of the most intensively studied groups of the catarrhine monkeys and our knowledge of their ecology and social behaviour therefore represents a useful yardstick against which our current knowledge of dolphins may be assessed. We describe here some strikingly similar features of behaviour seen during current systematic studies of factors influencing behaviour and communicative processes in free-ranging chacma baboons (*Papio ursinus*) and in captive and free-ranging Indian Ocean bottlenose dolphins (*Tursiops aduncus*). At this stage of research, qualitative descriptions of the behaviour of both species are still of significance, and it is hoped that this review will help to crystallize and delineate future avenues of research on both free-ranging and captive dolphins.

THE ANIMALS

BABOONS

Systematic observations of a troop of seventy-seven chacma baboons (*Papio ursinus* Kerr, 1792), ranging on the Honnet Nature Reserve at Tshipise in the northern Transvaal, were made by Saayman between March 1968 and November 1969 with the primary purpose of investigating the effects of ovarian hormones on social behaviour (Saayman, 1968; 1969; 1970a). The troop contained three adult males, fifteen subadult males, thirty-one adult females, fifteen juveniles and thirteen infants. Observations were generally made in the early morning and in the late afternoon when social behaviour was most frequent but the troop was sometimes followed throughout the day. After a period of habituation the observer could move freely amongst the baboons without disturbing them. An additional study was carried out for three months (April through June, 1969) on the inter-relationships between baboons and natural predators at Pretoriuskop and at Satara in the Kruger National Park. Observations were made from a Land Rover and baboon troops were followed throughout the day from dawn to dusk on successive days. The ecology and conditions of observation of baboons at Tshipise, the main study area, have been described in detail elsewhere (Stoltz and Saayman, 1970).

DOLPHINS

In March 1953 two free-ranging female bottlenose dolphins were encountered by Tayler at Fish Hoek, Cape, where frequent physical contact was established with both of them. This consisted of sitting astride the animal's back, surfing together, frolicking in one metre of water and towing by holding the dorsal fin. Although a young girl was particularly favoured and sought after by the dolphins when many bathers were present, it was possible to study them alone between 1300 and 1400 hrs., during which time various types of apparatus were employed. This encounter stimulated deeper interest in dolphins and motivated the ensuing research.

Observations of free-ranging dolphins, including *Tursiops aduncus*, *Sotalia lentiginosa*, *Lagenorhynchus obscurus*, *Stenella ephrosyne* and *Delphinus delphis* have been carried out by Tayler since March 1953. Vantage points overlooking the sea—Robbeberg (Plettenberg Bay), Chapman's Peak (Cape Town) and other suitable sites along the Tsitsikama Coast and Cape Peninsula—afforded a clear view to a depth of about 16 m., depending on water conditions. Dolphins were also watched from within a few feet from boats anchored in False Bay. Records were generally kept in writing and complementary commentaries were sometimes recorded. Sightings of dolphins ranged from a few minutes in length to continuous visual contact throughout the day.

Visual and acoustical records of two species, the Indian Ocean bottlenose dolphin (*Tursiops aduncus* Ehrenberg, 1833) and the humpback or speckled dolphin (*Sotalia lentiginosa* Owen, 1866), have been obtained in the Oceanarium, but the majority of studies have been

carried out on a group of *T. aduncus* (Haig, Lady Dimple, Daan and Dolly) members of which have successfully been maintained for periods ranging from one and a half to seven and a half years. Dolly, the first of this species to be conceived in captivity, was born to Lady Dimple in December 1968, following the successful introduction of the bull Daan to the females Haig and Dimple in November 1967. Dolfie, a bull captured together with Daan, lived for six weeks and a male calf, born to Haig in October 1969, did not survive. All humpback and a number of bottlenose dolphins died in the early phases of dolphin maintenance before the high stress factor of capture and transfer to a confined environment was fully appreciated. The surviving dolphins have retained excellent health, particularly since an appropriately spacious pool was provided for them in 1968. Their weights and ages are estimated as follows: Daan, 300 kg., 13 yrs.; Lady Dimple, 200 kg., 19 yrs.; Haig, 150 kg., 12 yrs.; Dolly, 45 kg., 1½ yrs. Other species, having access to or permanently with the dolphins, are listed in Table 1.

TABLE 1. List of species maintained in association with the dolphins.

Species	Common name
<i>Arctocephalus pusillus</i> (Rand)	Cape Fur Seal
<i>Spheniscus demersus</i> (Linnaeus, 1758)	Jackass Penguin
<i>Eudyptes chrysocome</i> (Forster, 1781)	Rockhopper penguin
<i>Phalacrocorax capensis</i>	Cape cormorant
<i>Morus capensis</i> (Lichtenstein, 1823)	Cape gannet
<i>Larus dominicanus</i> (Lichtenstein, 1823)	Black backed gull
* <i>Caretta caretta</i>	Loggerhead turtle
* Several species of sharks and large fishes	

* Not introduced to the Dolphin pool when the dolphins were transferred from the Main Tank.

Behavioural observations of captive dolphins and concomitant recordings of their phonation and sonar have been made at all times of the day and night in the Oceanarium since March 1963. Approximately two per cent of the records were made between 0200 and 0900 hrs. Approximately three hours per day were spent on visual observations and a daily average of one hour was spent on acoustical research. Acoustical work, however, was not conducted every day.

Equipment for recording and analysing dolphin phonation—sonar and whistle communication—consisted of a comprehensive range of hydrophones, transducers, six tape recorders, two oscilloscopes, two visual oscillograph storage displays, one pen writer, amplifiers, monitors, signal generators, speech simulators, coders, converters—such as analog to digital and amplitude modulated to frequency modulated converters—and other special control devices.

Between October 1962 and November 1968 the dolphins were held in the Main Tank (Plate 1), which was 21,5 m. in diameter, 4,2 m. deep, contained 820 800 litres of sea water, and had viewing ports (0,9 m. × 0,5 m. high) with 1,0 m. water depth at the top of the viewing ports. Water circulation was 5 500 litres per minute. The dolphins were transferred to the Dolphin Pool in November 1968. This pool, containing 4 742 400 litres of water, measured 61,5 m. × 55,4 m. at its widest points and was 4,6 m. deep, sloping up gradually to a depth of 5 cm. from "X" on the east wing and abruptly sloping to 2,5 m. from "Y" in the south bay. An isolation pool 10,8 m. × 6,8 m. × 5,5 m. and 0,8 m. deep with a 1,8 m. wide entrance adjoined the Dolphin Pool. Filtered sea water was pumped continuously into the pool from Algoa Bay

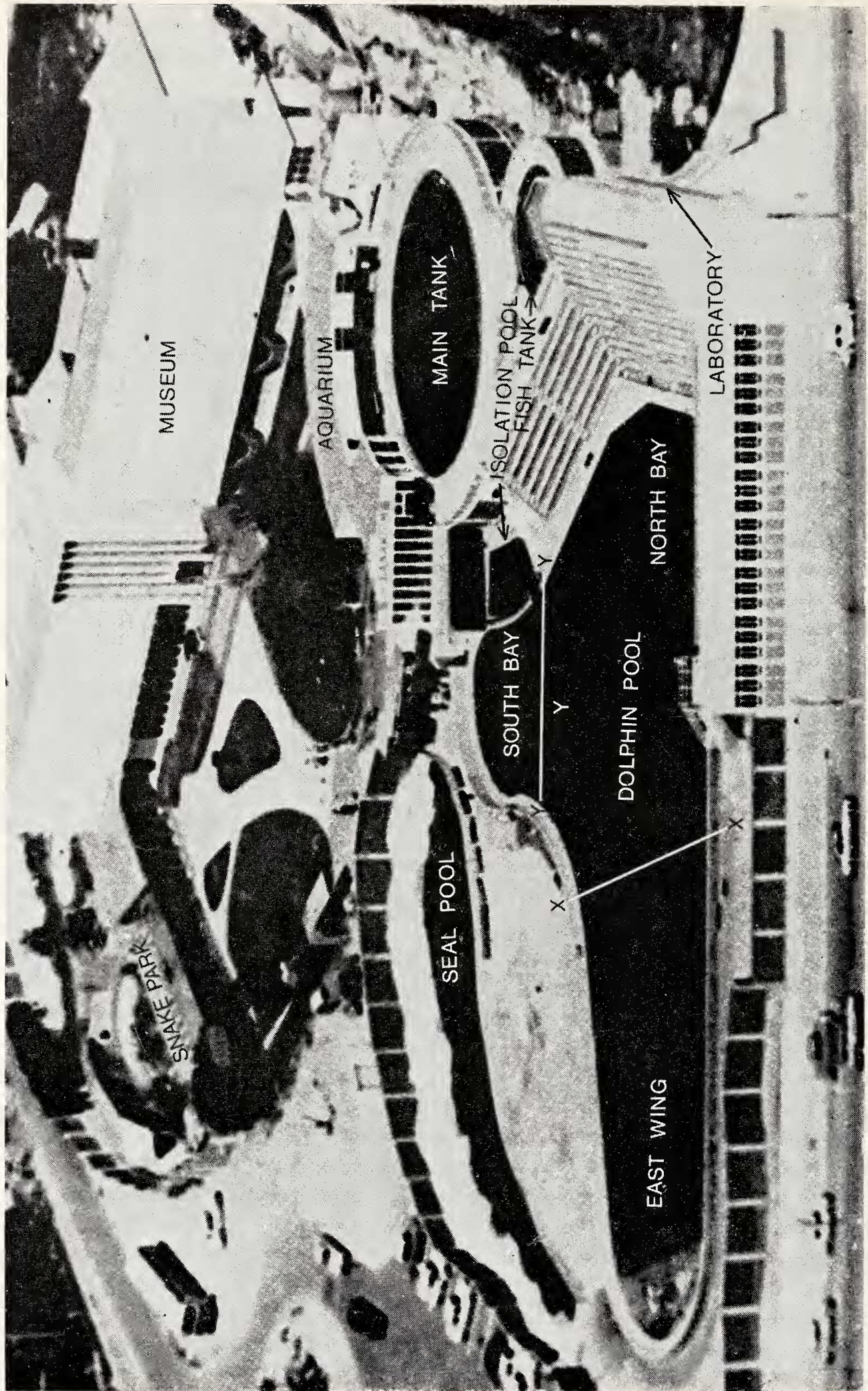


Plate 1. The Museum, Snake Park and Oceanarium complex. (Photo: P.E. City Council)

and additionally recirculated through a filter system at a combined rate of 11 856 litres per minute. Water temperatures reached a maximum of 77°F in summer and a minimum of 56°F in winter with an average of 64°F. A viewing port (1,8 m. × 0,6 m. high), 2,2 m. beneath the surface of the water, was situated in an observation room adjoining the main laboratory and enabled acoustical records to be made together with behavioural observations of the animals from under the water.

The financial requirement to display the dolphins to a paying audience was put to valuable use as it ensured a punctual and carefully controlled display twice daily at 1100 and 1530 hrs. These performances, contrived and conducted by Tayler, were informal and although the customary exhibition of retrieving objects, hoop-jumping, boat-towing and display-leaping was given, the manner and order in which the responses were executed was directly related to experiments on behaviour, intelligence, memory, sonar and communication. Sound recordings of concomitant dolphin phonation with complementary commentary were made at these times.

Food reinforcement during performances was usually necessary but the dolphins were always fed to capacity. In addition, supplementary meals were given between 0800 and 1000 hrs. and between 1600 and 2000 hrs. in cold conditions and during experimental and training periods. Live river bream (*Tilapia mossambica*) were periodically released into the pool to maintain food capturing ability. A list of fish species, fed whole to the dolphins, is given in

TABLE 2. Species of fish fed whole to captive dolphins (listed in order of availability).

<i>Common names:</i>	<i>Family:</i>	<i>Species:</i>
Reds/Gorrie	Pagellinae	<i>Pagellus natalensis</i>
* Hake/stockfish	Coryphaenoididae	<i>Merluccius capensis</i>
Pilchard/sardine	Clupeidae	<i>Sardinops ocellata</i>
† Maasbanker/kipper	Carangidae	<i>Trachurus trachurus</i>
Bream/Telapie	—	<i>Tilapia mossambica</i>
Mackerel	Scombridae	<i>Auxis thazard</i>
Kabeljou	Sciaenidae	<i>Johnius hololepidotus</i>
Bank Steenbras	Pagellinae	<i>Lithognathus mormyrus</i>
Shad/Elft	Pomatomidae	<i>Pomatomus saltator</i>
‡ Mullet/Springer	Mugilidae	<i>Heteromugil tricuspidens</i>
Soldier	Denticidae	<i>Cheimercies nufar</i>
Karpenter	Denticidae	<i>Argyrozona argyrozona</i>
Baardman	Sciaenidae	<i>Sciaena capensis</i>
White stumpnose	Sparidae	<i>Rhabdosargus globiceps</i>

* Head removed

† 1st Dorsal spine removed

‡ Eviscerated.

Table 2. Food fish were captured in quantities of up to 1 800 kg. by trawl, blast frozen to 0°F and, prior to feeding, thawed to the water temperature of the pool, but not exceeding 70°F. The weight of each fish varied from a few grammes to 1,8 kg. The average food consumption of a female dolphin was 11,4 kg./day (16,0 kg./day in the case of pregnant or lactating cow), with a maximum of about 20,5 kg. The bull dolphin consumed a daily average of about 13,6 kg. with a maximum of 31 kg. Daily vitamin supplements were added to the diet, concealed in the gut of fish, as follows: 1 000 mg. Vit. C (Ascorbic acid); 45 mg. Vit. B complex (B₁—2,0 mg., B₂—3,0 mg., B₆—0,5 mg., plus Calcium d-p antothenate 2 mg. and nicotinamide 15,0 mg.,

fortified with brewer's yeast); 100 mg. Vit. B₁ (Thiamine hydrochloride); 20 cc's. cod liver oil (Vit. A & D). Weekly supplements of 300 mg. ferrous gluconate and 50 mcg. Vit. B₁₂ (Cyanocobalamin) were added. In addition to the above, pregnant and lactating cows received Calcium plus Vit. D ("Calsuba", as prescribed). Half of the above doses were administered to the dolphin calf.

Infections such as enteritis, gastritis and septic wounds were treated orally with chloramphenicol (Chloromycetin, Parke-Davis) 1,5 times the human dose/kg. body weight. Extreme gastronomic cases were treated by intubation and injection. A problem in the Main Tank was the ingestion of foreign objects, such as plastic bags. An emetic concealed in a food fish (two teaspoons of copper sulphate) caused regurgitation of stomach contents in ten to thirty minutes. Constipation was treated with liquid parafin injected into food fish.

RESULTS

SOCIAL DOMINANCE

Baboons

The dominance hierarchy is a factor central to the understanding of the co-ordination of groups of monkeys (Carpenter, 1942). In recent studies, the functions performed by adult male baboons in maintenance activities have generally been categorized as dominant behaviours, including surveillance of the environment, defence of the troop during antagonistic inter-troop encounters and against attacks by predators, initiation and direction of troop progressions and prominence in sexual and intra-troop aggressive interactions. Dominance hierarchies amongst adult males have been described in *Papio ursinus*—South Africa (Hall, 1962a) and in *Papio anubis*—East Africa (Hall and DeVore, 1965). In forest-living baboons in Uganda, however there was no marked evidence of male dominance (Rowell, 1966) and the one-male social units of Ethiopian desert baboons *Papio hamadryas* could not meaningfully be related to a troop dominance hierarchy (Kummer, 1968a). Co-operation between adult males, however, emerges from the majority of accounts as a significant element in the organization of baboon social behaviour.

At Tshipise, it was difficult to rank adult males on a dominance gradient since there was no suitable criterion. Instead, the quantification of relevant behaviour patterns demonstrated that there were marked individual differences in the functional behaviour of the three adult males (Saayman, 1971). Male "Barker" displaced the two other adult males "Yogg" and "Sickle Tail" in the majority of individual aggressive encounters, but in severe fights Yogg and Sickle Tail supported each other and dominated Barker. Barker was involved in significantly more intratroop aggressive episodes involving all classes of baboons and was also prominent in the maintenance of vigilance. Yogg and Sickle Tail were in the forefront during antagonistic inter-troop encounters and when a strange adult male baboon was artificially introduced in the troop. Competition for receptive females was rare and Yogg, an old toothless male, was responsible for proportionately more mating and grooming behaviour with receptive females; Barker, the most aggressive male, completed significantly fewer copulations.

The three adult males were generally followed by groups of adult females and juveniles, but lactating females with small infants were especially prominent in the groups accompanying Yogg. The old male was frequently followed by eight or nine ambulant infants and large play groups gathered in his vicinity (Plate 2). Yogg, accompanied by a group of females with infants and juveniles, sometimes used a sleeping site far removed from that of the troop. The old male remained beneath the kopje while other baboons ascended to the main sleeping cliff. As darkness fell, Yogg led the group to an alternative sleeping site. During the day, Yogg influenced the direction of more troop progressions than did other baboons. Detailed descriptions of the contributions of the adult males to the social organization of the troop have



Plate 2. A group comprising a lactating female, juvenile (far right) and seven infants—more than half of the troop infant complement—gather in the vicinity of the old male Yogg.

been given elsewhere (Stoltz and Saayman, 1970). Female baboons were generally subordinate to the males, and they made no obvious, directly attributable contribution to the organization of troop activities.

Dolphins

Dominance hierarchies in dolphins were observed most clearly in captivity. Numerous observations, using order of feeding or order of performing learned responses as indices, indicated that the older female (Lady Dimple), introduced into the Main Tank thirteen months after Haig, had within seventeen weeks assumed the dominant position. When a food-fish was presented at an equal distance of two body lengths between the two cows, it was taken by Lady Dimple while Haig displayed only intention movements towards it. Throwing a fish 15 m. however, resulted in competition with a number of alternative outcomes. Threatening or fighting (chasing and raking with the teeth) occurred if Haig outstripped Lady Dimple and took the fish. In some cases when Lady Dimple emitted typical whistling sounds, Haig withdrew. When Haig took the fish in spite of phonation, Lady Dimple chased her until she dropped it or until she had either been bitten or pursued for about 120 m. Dominance was further reflected in the responses of the two dolphins to a simple ball-retrieving experiment. Each dolphin was trained to retrieve a brightly coloured ball. When both balls were thrown together, each dolphin returned its own colour without competition. If only one ball was thrown however, Lady Dimple always returned it, regardless of its colour. In these cases, she received a reward only for returning her own ball; her approach was typically slow and unenthusiastic when returning Haig's ball. When Haig's ball was thrown alone repeatedly, Lady Dimple retrieved

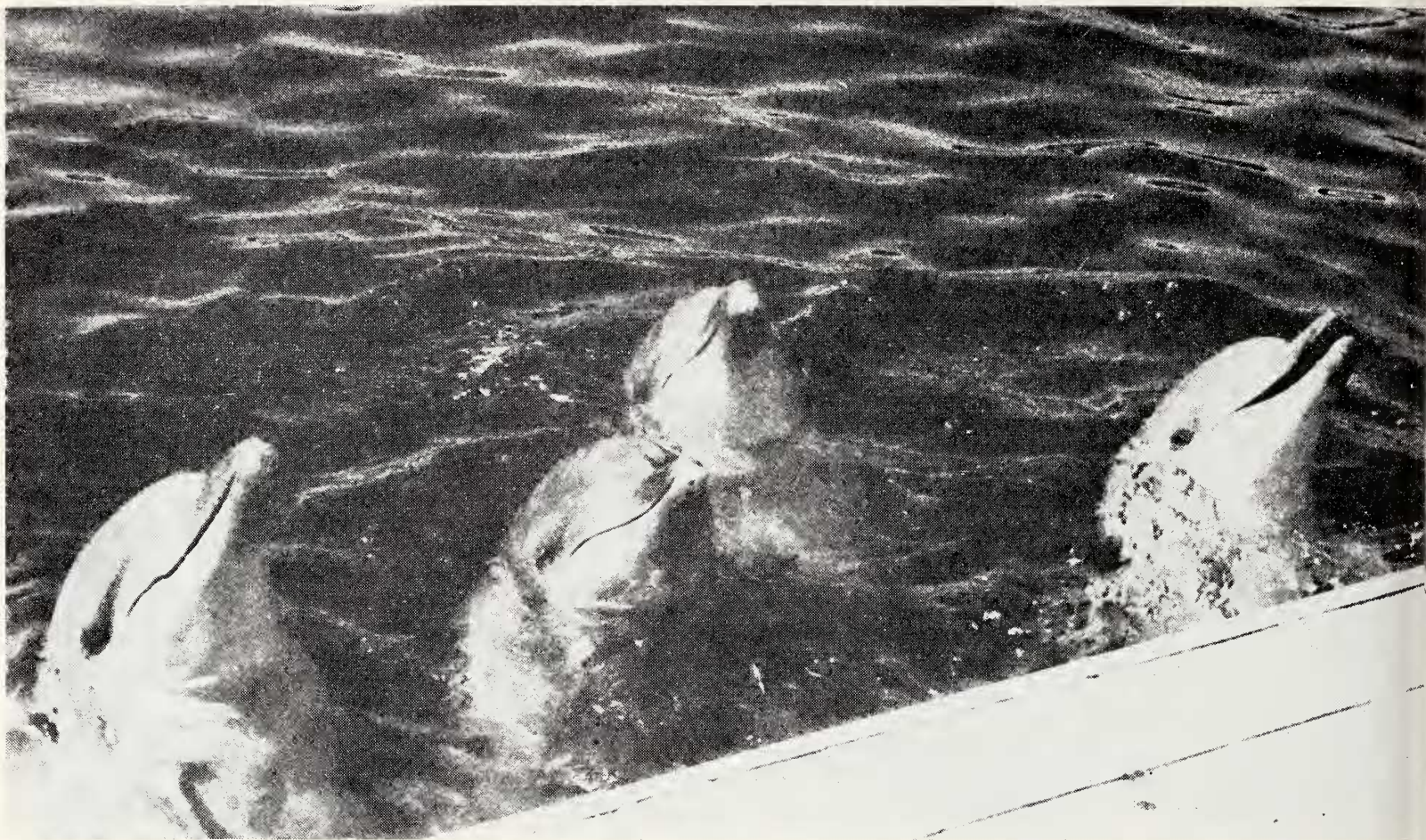


Plate 3. The waiting order of the dolphins during performances reflects the dominance hierarchy. Left to right: the bull, his temporarily favoured cow, the second cow and the female calf.

it only if Haig whistled or moved towards it, indicating that the suggestion of competition by the younger animal provoked the display of dominance. Similar results have been obtained in tests repeated thousands of times for more than six years. Further, Lady Dimple had the right of way either with or without apparatus and could generally displace Haig and occupy her position; any attempt to reverse this order resulted in chasing and biting. The above pattern did not alter until two bulls, Dolfie and Daan, were introduced to the tank: a cow favoured by a bull during courtship and mating sequences was dominant over the other cow provided that the bull was not more than 15 m. away. When favoured by a bull, Haig was sometimes threatened by Lady Dimple who, however, withdrew when counter-threatened by the bull. At the termination of the temporary pair bond the normal hierarchy between the cows prevailed: Dimple dominated Haig. The marked competition seen between the two cows was not observed in the dolphin bulls, Dolfie and Daan, which were captured together from the same group. Dolfie, the larger bull, asserted dominance actively mainly in food capturing and in the choice of cow and was in general given priority by Daan. Two underwater plastic balls, 38 and 23 cm. in diameter, filled with water and weighted for negative bouyancy, were placed in the tank. Dolfie preferred the larger ball and although Daan was permitted to play with it, he withdrew without sign of contesting ownership when Dolfie approached. Daan became the dominant dolphin in the tank when Dolfie died. He showed leadership in inspecting the new surroundings when transferred with Haig and Lady Dimple to the new Dolphin Pool; the dolphins circled the pool for several hours at high speed in a tightly knit formation with the bull in the lead. In general Daan dominated the group and had priority to playthings, food

and other incentives. He carried out characteristic "policing" manoeuvres (high speed swimming, display leaping, mock attacks) when anything unusual occurred, such as the intrusion of divers during maintenance operations in the pool.

The dominance hierarchy was reflected in the "waiting" order habitually adopted by the dolphins prior to and during performances or training sessions: Daan was generally to the left of the operator with Lady Dimple next to him and Haig on the far side. At nine months of age Dolly could move freely between the outside positions next to Daan or next to Haig (Plate 3) but was no longer permitted between the adults. It was necessary to conduct performances in strict accordance with the dominance hierarchy the dolphins had themselves established; bickering and chasing broke out if the dominant animals were not given priority in the presentation of the apparatus, rewards and the sequence of events.

Bottlenose dolphins, particularly older animals, were generally reluctant to physically contact unfamiliar apparatus. It was especially difficult to coax them to swim through a hoop, even if of large diameter, or to enter an enclosure. Lady Dimple, the dominant cow, usually intervened when the other dolphins were being trained. The compliant response of the dominant bull Daan to her interference—apparently causing his withdrawal from the apparatus by means of repeated whistling, threatening at the apparatus with open mouth and accompanying bursts of sonar pulses and, on occasions, physically impeding his progress—was particularly significant in regard to the dominance hierarchy. This influence by an elderly cow upon the behaviour of the physically larger bull indicated that dominance over group activities was not necessarily the sole prerogative of the bulls.

There was a difference between bulls and cows in their reactions to being displaced from their normal ranks in the dominance hierarchy. A displaced cow at first showed a marked increase in aggressiveness towards a subordinate dolphin, or even launched unprovoked attacks upon other species in the pool such as penguins or seals. Similar reactions occurred if the handler excluded and ignored a cow during experimental and training sessions. In contrast, the bull, when ignored by the handler, reacted by high speed swimming, jumping and general display behaviour. If this was also ignored, the bull ceased all activity and apparently withdrew from his overall dominant role; he permitted even the most subordinate dolphin to snatch food-fish presented to him. Although this situation was artificially created, it possibly reflects functional differences in the nature of the dominance hierarchies of bulls and cows in free-ranging groups.

The observation of feeding disputes and the adoption of strategic positions by dolphins during the herding of fish shoals (see under Responses to the Environment) suggested that dominance was a feature of the social organization of free-ranging as well as of captive dolphins.

SEXUAL BEHAVIOUR

Baboons

The organization of sexual interactions followed a similar general pattern in both species *P. ursinus* (Hall, 1962a, Saayman 1970a) and *P. anubis* (Hall and DeVore, 1965). Juvenile and less dominant adult males copulated with females in the early turgescence stage of the sexual skin during the follicular phase of the menstrual cycle and also in the early luteal phase, when the sexual skin had commenced to deturgesce. Dominant adult males, however, consorted exclusively with females at mid-cycle when the sexual skin was maximally swollen and conception was most likely. This pattern has been directly related to the male dominance hierarchy (DeVore, 1965). Competition for females, however, was rarely observed at Tshipise (Saayman, 1970a) or in troops of forest-living baboons in Uganda (Rowell, 1967): whereas females at mid-cycle were mounted more frequently by adult than by juvenile males it was also true

that females in the follicular phase of the cycle presented sexually to adult males significantly more frequently than they did to juvenile males. This suggested that females themselves played an active role in the selection of a sexual partner at specific stages of the menstrual cycle. Evidence from the Tshipise study indicated that it was not overt competition for receptive females along a dominance gradient but the ability of the adult males to stimulate consummatory sexual responses in the females which was a primary selective factor (Saayman, 1970a).

Consort relations at Tshipise were seen only between adult males and fully swollen females; these temporary pair bonds, ranging from 1—15 days, had a mean of 2.7 days. Consorting pairs were readily identifiable as the adult male partner became progressively less involved in troop activities and was sometimes led out of sight of other baboons by the female. The partners maintained close physical proximity, and when they were not engaged in mating or in grooming, they either fed within a few metres of each other or sat close together. This relationship was terminated shortly after the collapse in the dimensions of the sexual skin.

The organization of sexual interactions differed markedly from the above pattern in the hamadryas baboon: large and unstable groups gathered at isolated sleeping rocks at night but split up to forage during the day into one-male units consisting of an adult male leader and several females with their offspring. Units were highly stable and behavioural interactions between members of different units rarely occurred. Adult males did not copulate with or groom females from other units; females were immediately herded and retrieved by their leaders if they strayed. The close spatial association seen in other baboon types between males and females during consort relations at mid-cycle, therefore, was maintained at all times in the hamadryas group. True copulation by hamadryas males, as in the other species, however, occurred only when females were at mid-cycle (Kummer, 1968b).

Dolphins

Despite obvious agitation and fear of their new surroundings, the dolphin bulls copulated within ten hours of their netting and capture in the sea and introduction to the cows. A large proportion of the diurnal activities of the bulls was subsequently associated with sexual display. Sexual activity occurred in the early morning, at midday and in the late evening with a peak of activity near midday extending into the early afternoon. During courtship the bull displayed by high speed swimming (timed at about 35 k.p.h.), display leaping with flukes upturned when airborne and sharp, exaggerated turns and dives accompanied by explosive exhalations at each surfacing. These displays preceded physical contact with a cow, including gentle to vigorous rubbing together, massaging with flippers or flukes, swimming slowly with the bull in the lead, the flipper of the female touching his abdomen, and other characteristic postures and behaviour which culminated in copulation. A pair bond was formed and courtship displays and copulation occurred exclusively with the favoured cow for periods ranging from two to forty days. After a period of sexual inactivity, ranging from one to eight days, a bull recommenced displaying, generally to a different cow. Parading by the bull sometimes appeared to be initiated by the sexual advances of one of the cows, but in general it seemed to recur spontaneously. Courtship varied somewhat in detail, but followed the same general form.

The full pattern of copulatory behaviour was seen throughout the year, but in spring and in early summer (September to December) the frequency of copulation increased both in the wild and in captivity; cows appeared to be more receptive and permitted a greater number of insertions. Evidence derived from the study of the behaviour of the same cows under conditions both of sexual deprivation and in the company of bulls, suggested that they ovulated only in spring to early summer and that ovulation was induced by stimulation during con-

ulation. In the absence of a bull, the period of heightened receptivity was prolonged for two and a half months in a young cow yet it was abruptly terminated if copulation occurred and conception ensued. During the period of heightened receptivity both cows displayed agitated and neurotic behaviour for varying periods each year when no bull was present in the tank; this persisted for a maximum of four months in the young cow Haig. Further, at this time both cows displayed unusual cutaneous sensitivity to the areas surrounding the dorsal fin and peduncle. The onset of this behaviour was notably later each year.

Gestation in two cases in captivity lasted 342 and 351 days, judged from the onset of very marked behavioural changes and increase in appetite. Sexual play and copulation were observed during pregnancy but periods of interaction decreased progressively as the cow became more sluggish and apparently less receptive; copulation was disallowed altogether eight weeks prior to parturition. A brief period of sexual interest was shown by the cow three weeks after birth, but mother-calf inter-relations hampered the full expression of the copulatory pattern for a total of six weeks. A lactating cow copulated throughout the year and the number of insertions she permitted increased progressively until the normal pattern was seen six months after parturition.

The bulls did not fight for possession of the cows, but Dolfie had preference over Daan. If, for example, Dolfie displayed to Haig, when Daan was courting her, Daan withdrew and began to court Lady Dimple. Bulls possessed cows exclusively only during courtship; interactions seen during the limited period when two bulls were present in the tank suggested that the mating system was of a rotating, alternating kind lacking in permanent sexual bonds. In contrast, there was active sexual competition between the cows for attention, especially that of the dominant bull Dolfie. Lady Dimple was more likely to interpose herself and to respond to the display of a bull who was courting Haig, the less dominant cow. If fighting between the cows broke out, Dolfie chased off both of them—including Daan if he was involved. Sexual competition between the cows was more severe during the spring peak of heightened sexual receptivity.

Competition was observed in free-ranging dolphins in a sexual context. Characteristic courtship postures were seen in slowly progressing non-feeding groups. The typical sexual approach of dolphins brushing closely past each other, with white bellies showing beneath the surface, was a prominent feature of behaviour. Aggressive incidents involving side-swiping with the tail, threatening with open mouth and beating the surface with the flukes—a reaction probably indicating dissatisfaction—were also frequently observed. From time to time dolphins beat the water rhythmically with their flukes and occasionally two animals peeled off from the main group and chased each other out of sight of the observer, sometimes with a third dolphin in close pursuit.

SOCIALISATION

Baboons

An outline of development stages in the growth and maturation of baboons in the wild has been given by Hall and DeVore (1965). Observations in the present study were in general agreement with this account. A number of features directly relevant to this comparative report are mentioned below.

Soon after birth baboons commenced to show an interest in the black-coated infants, with their bright pink faces, ears and ischial callosities. Adult females in particular made a slow and cautious approach, lip-smacking and “presenting” (hind quarters) to the mother, before attempting to handle and sniff at the infant: a mother was reluctant to part with a very young infant, at times holding onto it while it was manipulated and investigated. As sensory-motor co-ordination developed, however, and the infant began to move a few metres from the



Plate 4. An adult female baboon runs with difficulty as she drags the carcass of her infant, attempting to hold it in the ventral clinging position.



Plate 5. A mother rests with her dead infant in the centre of the troop as the baboons return from the day range.

mother, other adult and juvenile females were allowed more frequent access to it. The colour of the coat commenced to change from black to grey at about four to six months of age. A limited number of observations indicated that the tending of grey-phase infants by other females occurred. On occasion, a mother spent hours moving and feeding over long distances alone while her infant was carried by another female. When retrieving the infant the mother approached the other female directly and without submissive gestures, took the infant from her arms, and suckled it. Several mothers with infants and other females with detumesced sexual skins regularly clustered together in grooming groups, often in the vicinity of an adult male. It is likely that close associative bonds were formed between adult females and infants as the latter played and romped over the adult animals during these periods. It was not possible, however, to investigate this aspect of development systematically in a large troop with unmarked individuals.

Instances of female baboons carrying the carcasses of infants for a number of days before discarding the decomposed remains were observed both at Tshipise and at Pretoriuskop (Plates 4 and 5). On one occasion at Pretoriuskop a subadult male picked up and groomed the carcass of an infant and then carried it for a short period after it had been discarded by the mother. In general, however, other baboons did not pay much attention to the carcass.

Males interacted with infants far less often than did female baboons. Nevertheless, there was a striking association between Yogg, the old toothless male, and lactating females (see under *Social Dominance*). If a mother with an infant was attacked and bitten by any baboon this old male immediately went to her assistance. The two other adult males were less concerned with mothers and infants during routine daily activities; the protective function performed by adult male baboons during times of stress or uncertainty, however, is well known (see Plate 6).

Older infants and young juveniles regularly assembled in the close vicinity of adult males and associated clusters of females and played in groups on the steep cliff faces or in the high



Plate 6. The protective function of adult male baboons: at the unexpected appearance of the observer, an adult male carries off a young infant, which has strayed from its mother.



Plate 7. Competition between juvenile baboons for novel objects: a juvenile, running erect on hindlegs, eludes its pursuer.

branches of trees. Mock-fighting and wrestling was frequently observed. A young baboon, leaping and clambering about the rock crevices, often fell when another, tugging from below at its fur or tail, dislodged it and assumed its position. Young juveniles played for long periods with inanimate objects such as stones, snail shells and dead vines or creepers (Plate 7). As in most games, the emphasis was on group interaction and several animals chased the baboon in possession of a novel object. Sometimes, however, a single juvenile carried an object for long periods without being interfered with or chased. Games became more rough as baboons grew older. Juvenile females withdrew to grooming groups and frequently played with black or transitional phase infants or groomed their mothers. Play decreased markedly when animals matured sexually; young females with sexual swellings and males with barely visible testicular development rarely played, although subadult males sometimes joined sporadically and roughly in male juvenile play. Adult animals very seldom played and then did so only briefly with very young baboons. Sexual mounting was not a prominent feature of play behaviour. Nevertheless, young juvenile males responded to the "presentations" of females early in the follicular phase of the menstrual cycle; this was true even of male infants about one year of age which, although they had difficulty in mounting, sometimes evoked full consummatory responses in females. Sexual interactions in immature females were not often seen.

Dolphins

Dolphin calves are capable of swimming to the surface to breathe shortly after birth and of keeping pace with their mothers (McBride and Kritzler, 1951; Tavalga and Essapian, 1957).

Dolly, Lady Dimple's calf, generally swam alongside and slightly above the centre-line of her mother; for approximately ten per cent of the time she swam underneath and slightly to the rear of her mother in the suckling position. Suckling took place while the animals were swimming, the cow turning on her side to make a mammary slit available to the calf during the first two weeks after birth; thereafter the calf learned to turn sideways to align itself for suckling.

Four days after birth Dolly was reprimanded by Lady Dimple for swimming too far ahead; when the calf failed to respond to phonation, she was nipped on the flukes and returned instantly to the suckling position. In free-ranging groups, a dolphin calf sometimes lost contact with its mother when the adult animal veered suddenly away; the calf continued to progress in the original direction until it was retrieved, or joined another adult. On two occasions Dolly collided with the side of the tank when Lady Dimple changed direction suddenly and it seemed that the cow restrained the calf from wandering too far from her until it had learned to make adequate directional responses to the environment. Dolly began to emit her first whistles and sonar pulses at eight days of age and four days later she was permitted to swim with Haig while Lady Dimple fed.

If perceptual development is a prolonged process in these mammals, calves are likely to strand on the beach if not adequately cared for when bottlenose dolphins are feeding in the surf. It was striking that calves were never seen in the surf in such groups: as a mother veered off to enter the surf, her calf immediately joined another adult dolphin which circled in the deep water just beyond the breakers until the mother returned, when the calf rejoined her. It was interesting, therefore, that Dolly was at first not permitted by Lady Dimple to approach the shallow end of the pool at all. However, she was later permitted to spend daily periods of up to an hour and a half swimming and playing in the shallow area with Haig. After prolonged exposure to these conditions she was permitted by Lady Dimple to approach the shallow end alone, and in fact learned to use it as a refuge when reprimanded and chased by her mother. When she was between two weeks and two months of age Dolly strayed several times from the adult dolphins; she emitted typical acoustical signals which, on the majority of occasions, were responded to by Haig, who retrieved her and returned her to her mother. As Dolly grew older, she learned to return directly when her mother Lady Dimple emitted homing signals in response to Dolly's repeated calls.

Haig was permitted to chastise Dolly at nine months of age and was dominant over her first of all in food capturing and later in priority of position during performances. When suckling attempts by Dolly inadvertently disrupted the sexual advances of Daan to Lady Dimple, the bull sometimes jostled or struck his flukes towards the calf; this mild display of aggression by the bull provoked a severe reprimand from the mother, Lady Dimple, who threatened him with open mouth, jerking her head from side to side, sometimes with accompanying bursts of sonar. She sometimes chased him, snapping at him as he beat his flukes in an effort to give way. Daan did not react to this maternal defence for the first six months after Dolly's birth, but thereafter he retaliated and Dolly sought protection with Haig until the dispute between Daan and Lady Dimple had been settled.

When some startling event—such as a seagull swooping low over the tank—caused Dolly to take fright, she fled either to her mother or to Haig, and only under conditions of extreme fright went to Daan if he was nearest. In the latter event, she retreated to her mother at the first opportunity when all adults had formed up in line-abreast formation, transferring from beneath Daan's belly to Lady Dimple, via Haig if she was next in line. Dolly in general avoided Daan until she was six weeks of age.

A layer of post-natal skin, slate grey above to yellow cream below, commenced to peel off Dolly nineteen days after birth. The process was completed after three weeks, revealing the normal colouration of a young bottlenose dolphin with light-grey dorsal surface and the contrasting light- and dark-coloured symmetrical markings on the head, throat and ventral surface. Dolly and Haig did not associate extensively away from the mother before the post-natal skin was shed. Dolly received the first deep rake marks from the teeth of an adult dolphin approximately three weeks after the skin had peeled off completely and four days later she played extensively with Daan, for the first time, for approximately two hours. When Daan and Lady Dimple recommenced copulating Dolly and Haig played together in the shallow end of the pool. Daan displayed sexually to Dolly when she was eleven months of age, and the full pattern of copulatory behaviour, including insertion, was observed. Thereafter Dolly, although sexually immature, associated closely with the adult animals during courtship and frequently displayed behaviour resembling the adult sexual pattern, suggesting that imitative learning was taking place.

A bull calf, born to Haig, died shortly after birth; it was taken below, pushed to the surface, struck lightly and nuzzled by Lady Dimple several times. Haig then carried it in her mouth (Plates 8 and 9) for five days before relinquishing it in a state of advanced decomposition.

The captive bottlenose dolphins showed a marked propensity to play; this was true particularly of younger animals, but playing was prominent in the daily activity cycle of the mature dolphins as well. Dolly was much occupied with the investigation and exploration of novel objects such as cleaning nets, penguins, water inlets and drains. The dolphins developed games with the other species in the tank as focal points of activity. They took it in turns to chase a penguin and to prevent its exit from the water. A single dolphin swam close to the penguin at speed while the others followed behind it; after a few minutes a second dolphin took over the active role. Some play activities were clearly social in nature, such as when



Plate 8. Haig, accompanied by Lady Dimple, circles the pool with difficulty, her dead calf clasped firmly with her teeth.

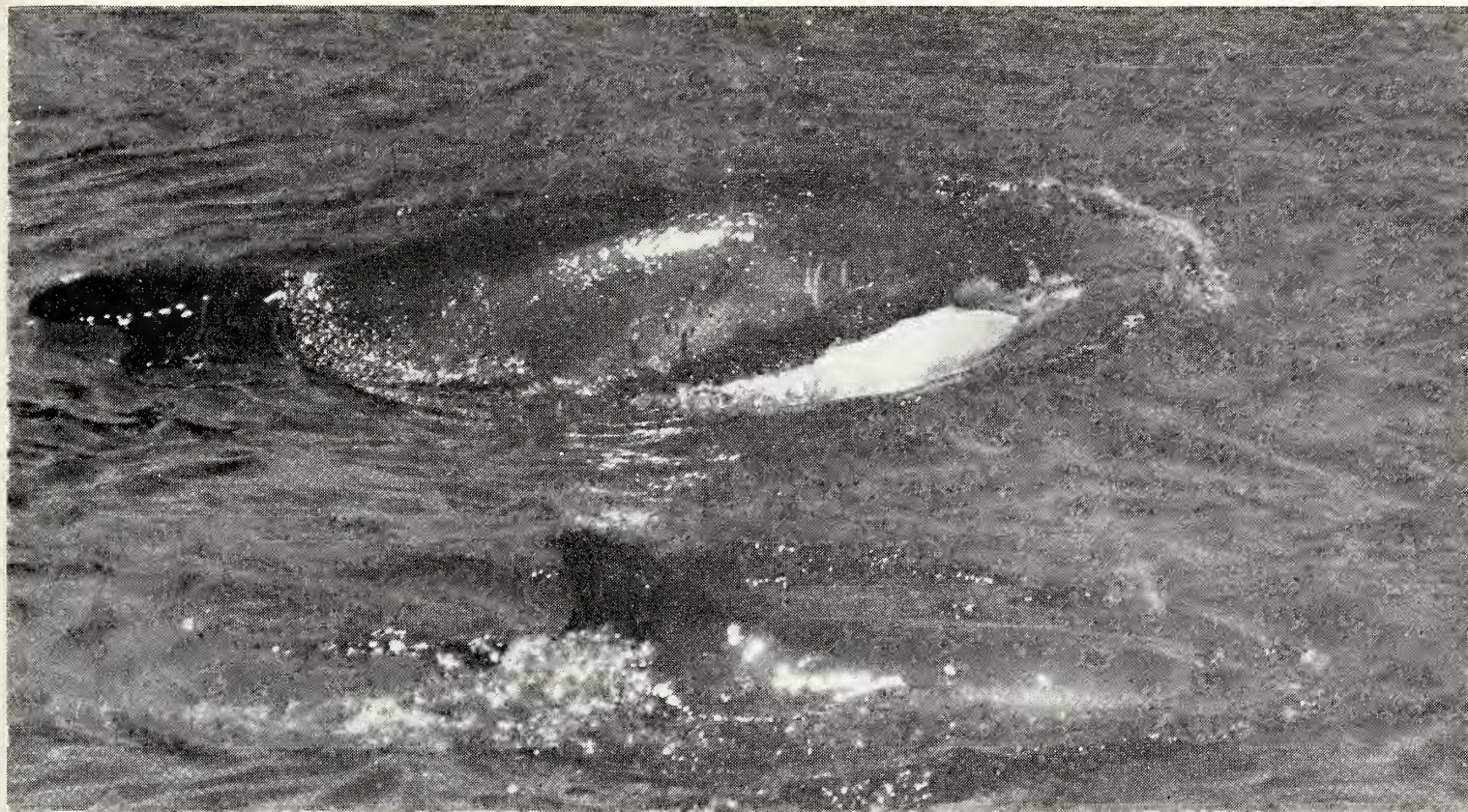


Plate 9. Haig, carrying her dead calf, is accompanied by Dolly. Note the greater forward displacement of water ahead of Haig; this did not prevent her from carrying the carcass for five days.



Plate 10. Haig playing with a stone. Dolphins invent a variety of games with inanimate objects.



Plate 11. Lady Dimple playing with her water-filled ball. The dolphin cows, unlike the bulls (pg. 11), did not allow other dolphins access to their playthings.

dolphins chased each other, but they frequently played on their own, tossing and retrieving a variety of objects such as fish skins, bits of seaweed, stones or balls (Plates 10 and 11). Turtles were treated as balls, pushed down through the water and bounced on the bottom of the tank. Elaborate manoeuvres were carried out while swimming, balancing an inanimate object, such as paper or a feather, allowing it to slide down the length of the body only to be caught and held by flippers or flukes. Dolly, the youngest animal, exhibited the most marked play and exploratory activity whereas Lady Dimple, the oldest dolphin was the least exploratory of the group, although she played extensively with her calf Dolly.

Play groups, rarely seen in free-ranging dolphins, generally consisted of two to four immature animals disporting together, leaping over non-participating adult animals, chasing each other, head jerking and side-swimming. Playful activity was identifiable in the wild by virtue of its vigorous yet non-aggressive nature; however, in adult animals it was not readily distinguishable from sexual behaviour except when single animals played, tossing scraps of seaweed or fish skin, very much as did the dolphins in captivity. When butterflies were numerous on the coast, all age classes of dolphins, with white bellies showing and zigzagging at speed, frequently chased them when they flew out over the water.

RESPONSES TO THE ENVIRONMENT

Baboons

Baboon troops use regular sleeping places situated either in steep cliff faces or in high trees where the animals are relatively sheltered from the elements and safe from predators (Hall, 1962b; Hall and De Vore, 1965; Kummer, 1968b; Altmann and Altmann, 1970; Stoltz and Saayman, 1970). The choice of sleeping place varied, alternating between a number of suitable sites, and was influenced by factors such as the availability of water or by interactions with neighbouring troops of baboons (Stoltz and Saayman, 1970). A troop of baboons at Pretoriuskop on occasion remained in the veld to sleep in trees instead of making for the customary sleeping places in the granite kopjes. Gradual movement of chacma baboons away from the sleeping site commenced at first light. The time of descent and full progression to the feeding ground was affected by summer or winter periods, availability of food and water, inter-troop interactions and encounters with predators in the vicinity of the sleeping site. Times of departure in winter were usually later than those in the summer; the animals sat on the rocks in the sun sheltered from the wind until the heavy dew had dried from the grass.

At Pretoriuskop well-worn tracks marked the routes to the feeding grounds. The top of the kopje at Tshipise was criss-crossed with many baboon tracks inter-connecting the alternative sleeping sites. The routes followed on successive day ranges varied by clear patterns were discernible, especially in regard to the foci of feeding and drinking activities. The factors influencing the direction of the day ranges were probably as varied as those affecting the time of full progression to the foraging ground; the length of the day range was inversely correlated with daily temperature at Tshipise (Stoltz and Saayman, 1970). In addition, it was possible that individual baboons played a positive role in the "decision taking" process, since the Tshipise troop generally did not move long distances unless accompanied by the old male Yogg. It also seemed likely that a novelty variable affected the alternation of the direction of day ranges.

The organization of troop progressions in East African baboons has been related to functions of vigilance and defence (Washburn and De Vore, 1961; De Vore and Washburn, 1963; Hall and De Vore, 1965): the baboons adopted an invariable order of progression en route to the feeding grounds and on the return to the sleeping site at dusk with the dominant adult males and females with young infants and juveniles protected in the centre of the troop, and the less dominant males and larger juveniles on the outskirts forming a defensive cordon. In chacma baboon troops there were two clearly distinguishable modes of progression: the first was seen when the baboons were moving rapidly from one area to another in a relatively compact group. When baboons used roads they spread out four or five abreast in a long file; when moving along narrow baboon tracks the animals sometimes moved virtually in single file. Secondly, in contrast, a foraging troop was widely dispersed in scattered groups often extending over three hundred metres or more (Fig. 1). In troops at Tshipise and at the Kruger National Park females with young infants tended to associate closely with adult males during troop movements. The mode of progression appeared to be related to the rate with which the animals were moving: the tightly knit, compact formation was used when troops were moving at a fast, sustained rate from one place to another. As the baboons began to forage either through thick bush coverage (Tshipise) or across open plains (Satara, Kruger National Park), they spread out and the pace became much slower. There was a tendency in certain troops for adult males to occupy positions both in the vanguard and in the rear of the troop (Fig. 1).

How the deployment of chacma baboon troops related to predation pressure, if at all, was not very clear. Indeed, the reaction of baboons to predatory animals was not predictable. For example, jackals have been listed as potential predators of baboons (DeVore and Hall,

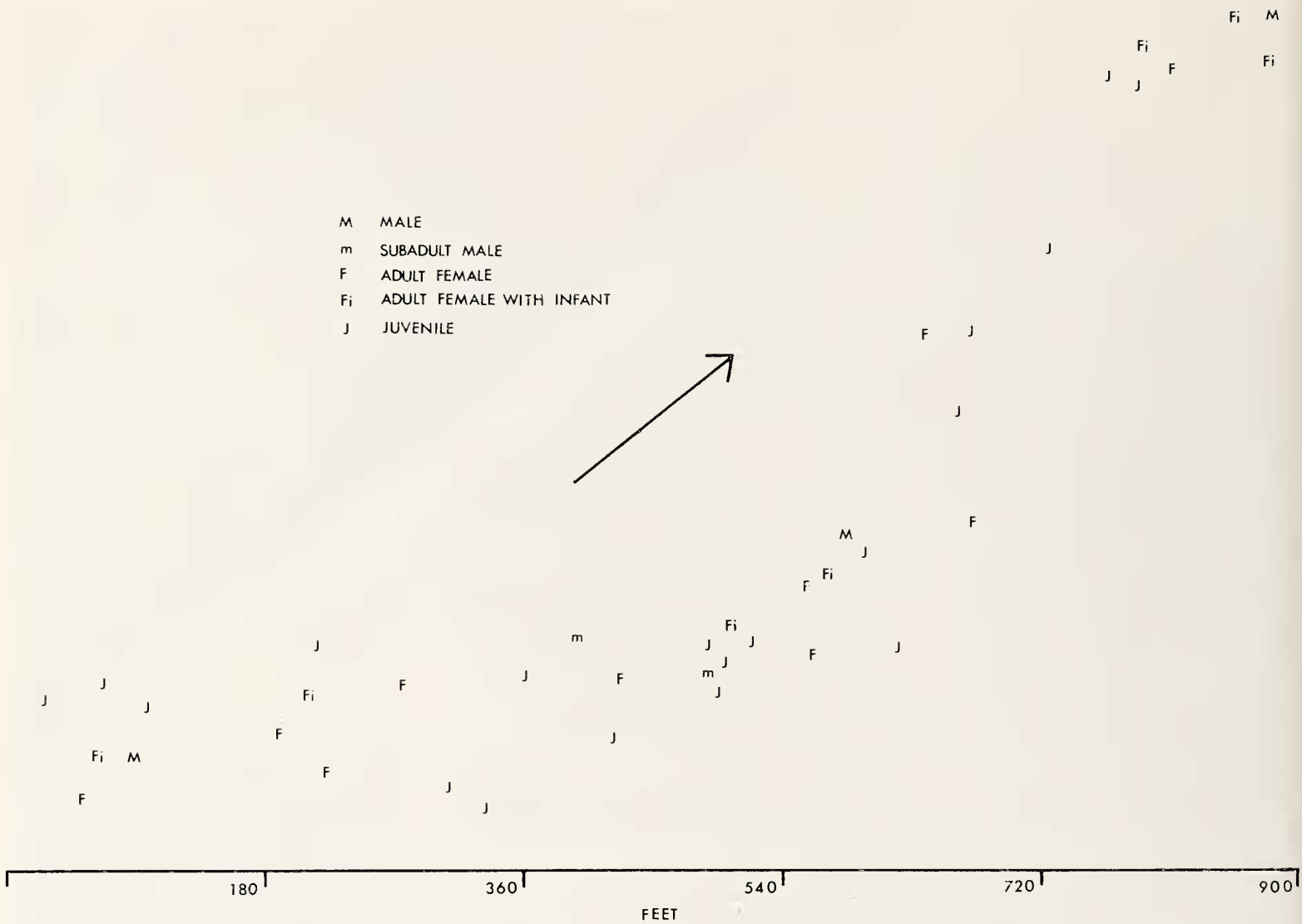


Fig. 1. A widely dispersed troop of baboons foraging across open veld. Note the adult males to the front and rear of this progression.

1965), whereas a sequence of events closely resembling play behaviour between three adult blackbacked jackals *Canis mesomelas* and the juveniles of a troop of baboons was observed at Pretoriuskop (Plates 12 and 13). The initiation of apparently playful sequences of behaviour by the jackals and the absence of aggression and marked indifference of the adult baboons has been reported in detail elsewhere (Saayman, 1970b). Flight from lions by baboons foraging on open veld at Satara appeared random and resembled the precipitate, disorderly flight seen when baboons were chased by humans with firearms at Tshipise (Stoltz and Saayman, 1970). In marked contrast, a troop of baboons, advancing *en masse* barking and threatening over flat terrain, drove away a lioness and cubs from a resting place beneath a baboon sleeping site at Pretoriuskop. Doubtless the combined action of a troop of baboons acted as a deterrent to predators and the survival of a number of severely crippled individuals in troops at Pretoriuskop (Plates 14 and 15) attested to the effectiveness of the protection afforded to members of the baboon social group.

Troops ranged over relatively constant areas and there was considerable overlap in the home ranges of different troops, especially in those areas containing sleeping, drinking and feeding sites. Movement of baboon troops into new terrain, however, occurred (Hall, 1962b;

Altmann and Altmann, 1970), and at Tshipise this seemed to be related to the seasonal appearance of honey dew on the leaves of the mopane trees *Colophospermum mopane* and also to seasonal alterations in the water supply (Stoltz and Saayman, 1970). In July 1968 the troop left Tshipise and moved into the sandstone ridges far to the south of their normal home range limits. The baboons followed a route along a belt of mopane trees, feeding heavily from the leaves. Antagonistic encounters with other baboon troops at sleeping and drinking sites appeared to be an important factor leading to the return of the troop to its haunts at Tshipise.



Plate 12. A juvenile male baboon backs away as it is stalked by a jackal. In the background, a second jackal approaches while an adult female and juvenile baboon look on.



Plate 13. The jackals did not attempt to initiate their playlike activity with adult baboons. The baboon in this confrontation is an adult female.

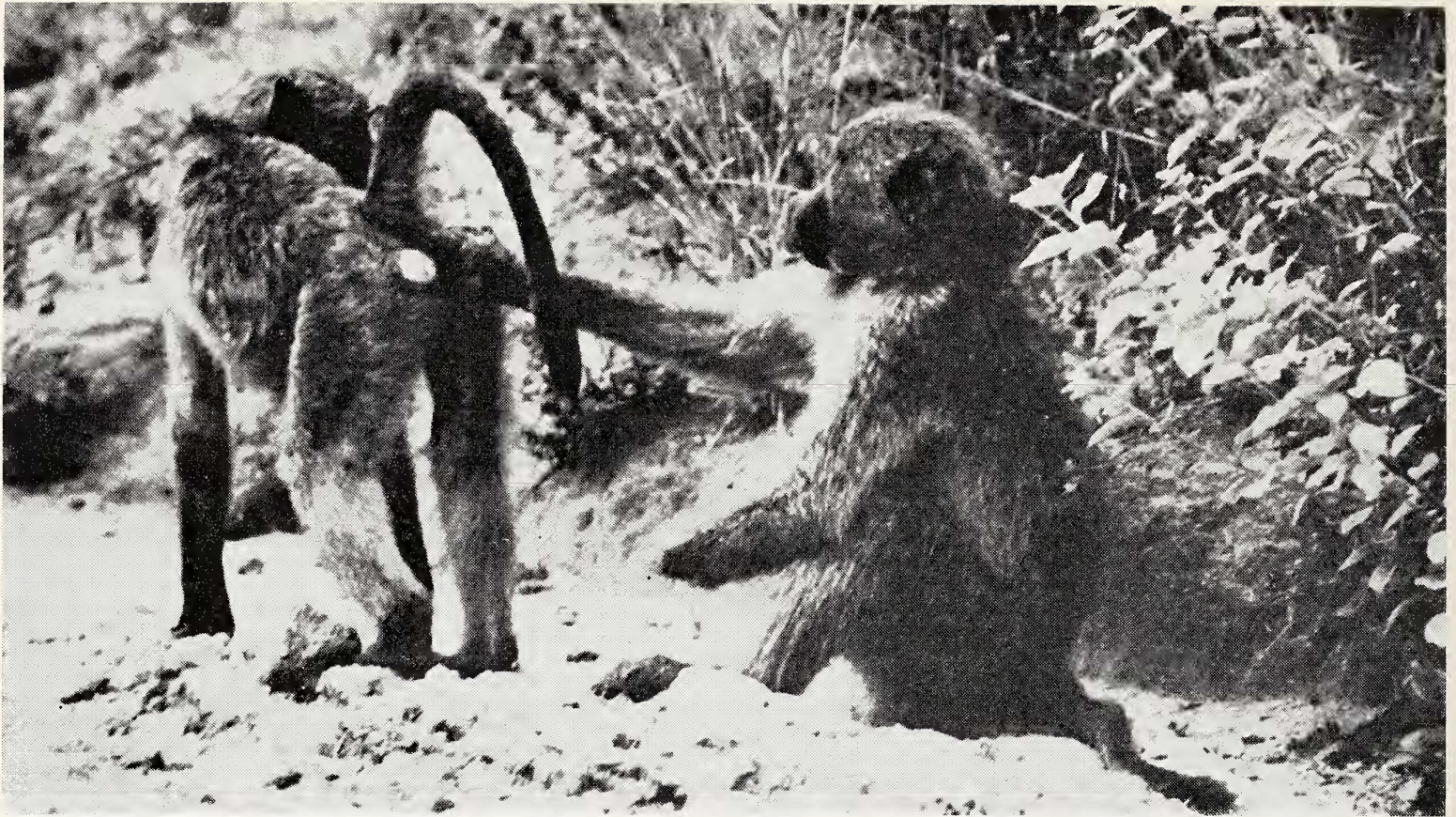


Plate 14. Severely handicapped animals may survive in baboon troops. A juvenile female presents her hind-quarters and is touched in greeting with the good hand of the maimed individual.

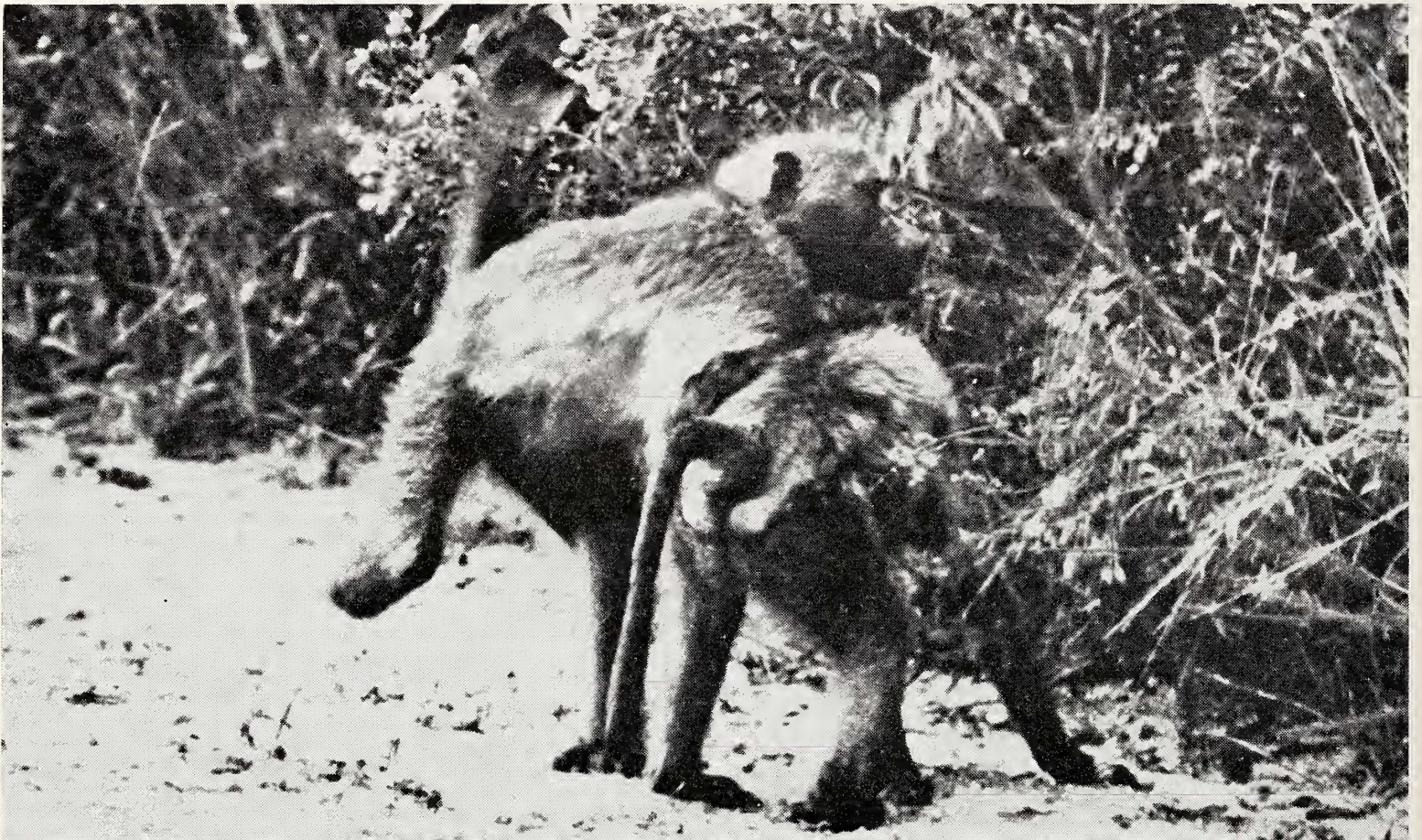


Plate 15. Play activity follows the greetings ceremony between these two juvenile females, although one of them is handicapped by the loss of the left hand and right foot.

A second departure from the normal home range occurred a year later. The new route again passed through belts of mopane trees and the animals stripped off the leaves and fed from them as they progressed.

The number of baboons in troops at Tshipise and Pretoriuskop ranged from about twenty to eighty individuals. Adult females outnumbered adult males in all but one troop, as is reported to be the case in the majority of multi-male troops with the exception of the yellow baboons studied by the Altmanns. High rates of migration by adult males have been reported by Rowell (1966) and Altmann and Altmann (1970) and the Altmanns have suggested that this may partially determine the disparate adult sex ratios, since migrating males may spend a solitary period unattached to any group. The regulation of troop size and adult sex ratio may therefore be related to the question of whether baboon troops are stable, impermeable social units. Adult males occasionally left their own troops at Pretoriuskop—though not at Tshipise—and joined neighbouring groups of baboons. At Tshipise it was possible to introduce females, trapped from neighbouring troops and marked with collars, into the study troop whereas an adult male, similarly marked and released, was ousted by the adult males (Stoltz and Saayman, 1970). Some of the females subsequently left the study troop, attached themselves to neighbouring troops for several months and returned again to the Tshipise troop. It has not yet been determined whether unmarked females or immature animals were involved in similar movements. At Pretoriuskop marked tolerance existed between certain troops, but not between others. Two troops frequently utilized the same kopje as a sleeping site and sometimes ranged together so intermingled it appeared that only one troop was present. A third troop, however, was sometimes chased from the sleeping kopje and spectacular, tumultuous fights were seen when all three troops had converged on the kopje at dusk and the two troops combined to drive the third away. These observations suggested that an original, large troop might have split into two distinct groups; if this were true, movement of individuals between specific troops might have been possible because of the relative familiarity of the respective animals. Lukas Stoltz has trapped and marked several troops in a reserve at Loskopdam in order to carry out a long term investigation of these and related questions.

Dolphins

When a dolphin was introduced into captivity it kept constantly on the move. Locomotion slowed down at night and over a period of days the pace became progressively slower until the animal came almost to a halt but lost its balance and began to sink, resulting in strong swimming movements. The whole process was repeated until eventually the dolphin could come to a graceful halt and remain motionless on the surface. Dolfie and Daan were observed systematically at night following their capture; within two weeks they had learned to float while stationary on the surface, and this was accomplished first by Daan, the smaller, lighter animal. These findings suggested that similar cessation of locomotion did not occur in free-ranging dolphins. Further, after the birth of Dolly, Lady Dimple began again to keep continuously mobile; when she recommenced stopping for brief periods at night (three minutes increasing gradually to about fifteen minutes) Dolly circled her slowly until after six weeks she had learned to remain stationary. The primary difficulty experienced by dolphins appeared to be inadequate control of bouyancy; they sank sideways, apparently dragged under by the weight of the heavy motor muscles while making efforts with the flippers to right themselves. During the day the pace of newly captured dolphins slowed gradually but only two weeks after they had learned at night to remain motionless on the surface did this pattern become a regular feature of their diurnal activity cycle.

Whereas the above observations indicated that free-ranging dolphins did not remain motionless at night, it was nevertheless possible that they returned regularly to specific areas.

A concerted effort was made on moonlit nights over many years and at different localities to observe nocturnal behaviour: the very limited number of sightings indicated that dolphins frequented certain areas of Algoa, Plettenberg, False and Hout bays at night. These observations, however, were possibly biased by the peculiar limitations of nocturnal conditions.

The captive dolphins almost invariably came to rest in the same part of the tank. Further, regular patterns of subgrouping were seen at night: the cows Haig and Lady Dimple favoured an area near the water inlets and feeding platform in the Main Tank, whereas the bulls took up a position together in another quadrant. Both areas were bathed in neon light, whereas the rest of the tank was less illuminated. When a dispute occurred between the two bulls, the subordinate bull Daan rested in the third, poorly illuminated quadrant. When the animals were moved into the Dolphin Pool after the death of Dolfie, the dolphins rested together except on those occasions when Daan split off during a pair bond with a highly favoured cow. The dolphins rested with intermittent periods of very slow progression after the lights were switched off before midnight.

It was not possible to formulate reliable general conclusions concerning the ranging and dispersal of unmarked and unknown dolphins in the wild. However, observations of dolphin movements with a view to capturing suitable animals indicated that a group of about twenty dolphins, identifiable by the characteristically inclined and notched dorsal fin of the largest animal, frequented an area in Algoa Bay approximately twenty miles in extent for several

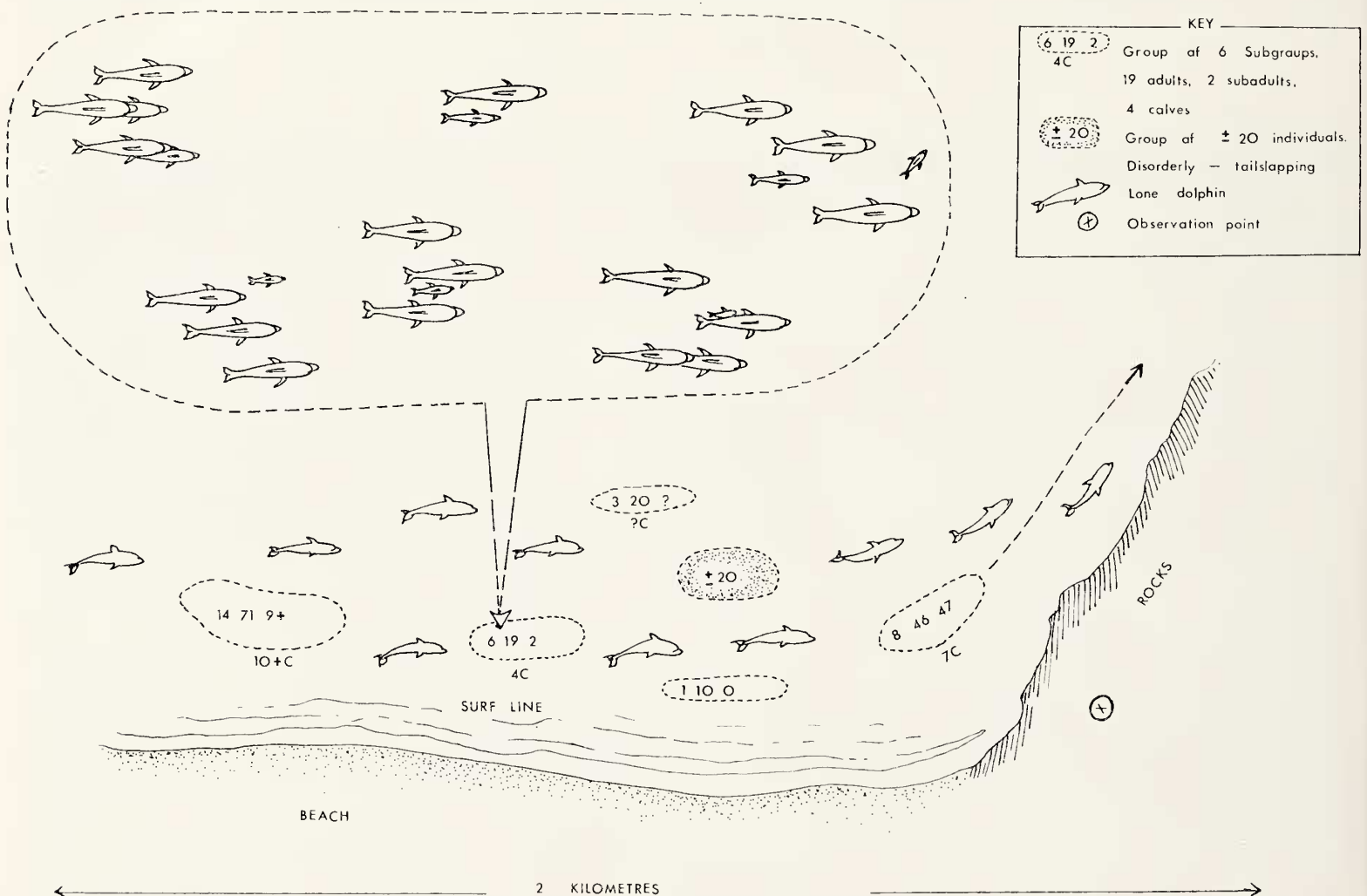


Fig. 2. A school of slowly progressing bottlenose dolphins comprising groups of subgroups with scattered lone individuals. Counts were made as members of each subgroup surfaced in synchrony as they passed in clear water beneath the observer.

consecutive days. Two bulls were subsequently netted from the rear of this group as the dolphins moved parallel to the shore in the shallows in line-astern formation. The larger of the two (Dolfie) had an inclined notched dorsal fin, closely resembling that seen in the dolphin at sea and it is likely that they were the same animal. Using the shape of the dorsal fin and the relative proportions of the head as criteria, close-range observations of this group indicated that it consisted predominantly, if not entirely of bulls. Similarly, in an earlier capture operation when Haig was taken, she was closely associated with another cow. Out of a total of five capture operations the following animals accompanied each other and were netted together: (i) an adult cow and a subadult cow, (ii) two adult cows and a subadult cow, (iii) two adult cows, two subadult bulls and a juvenile bull, (iv) two adult bulls, (v) two adult bulls. In both cases (iv) and (v) the bulls were believed to have been taken from the rear of their groups. These findings supported the subjective impression that of the many possible combinations of the four age classes (adult, subadult, juvenile and calf) the following associations did not occur: immature dolphins only and immature dolphins accompanied by bulls.

The spatial organization of dolphin schools varied in relation to time of day, number of animals and form of activity. A school of dolphins in transit, comprising several distinct

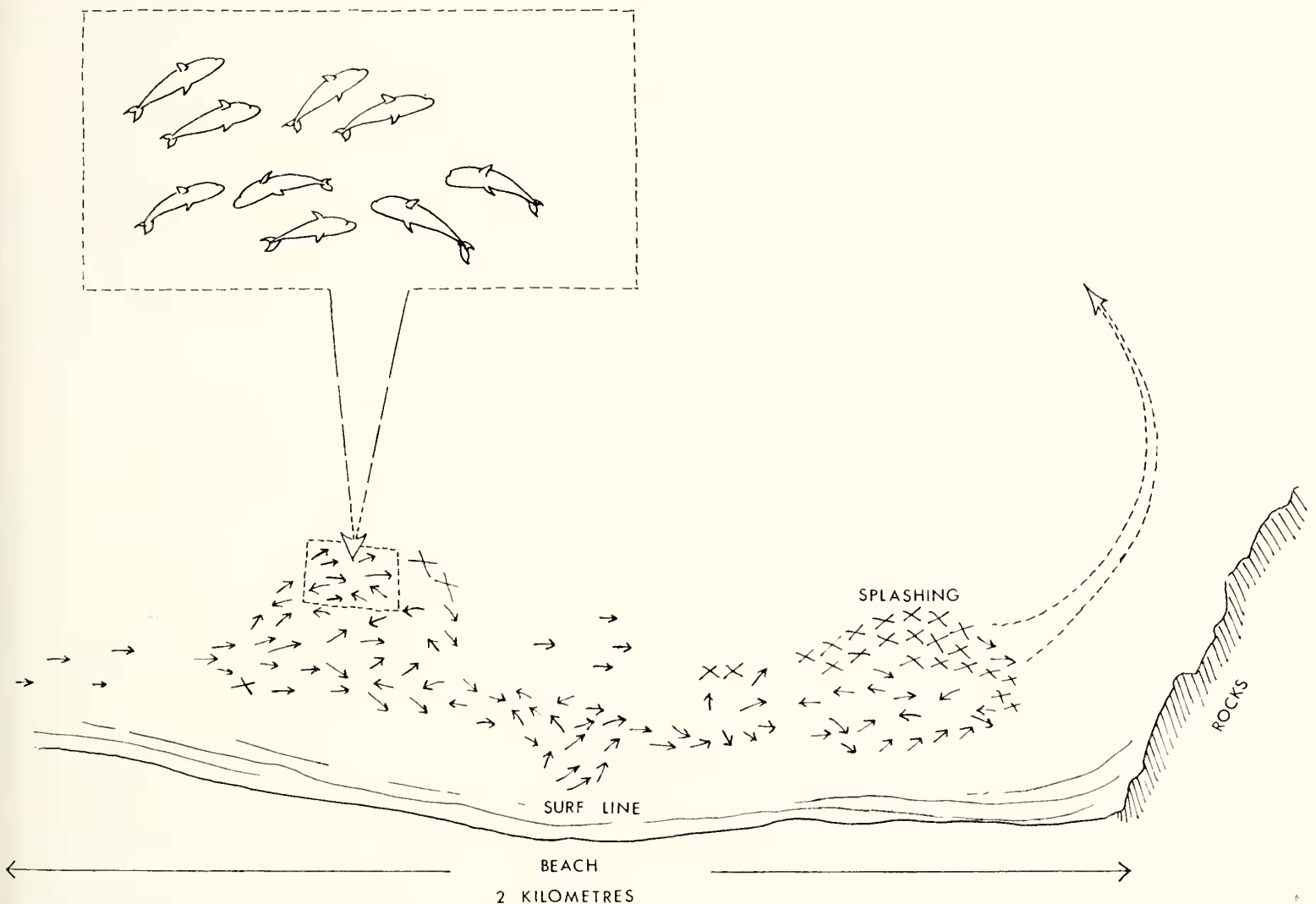


Fig. 3. A school of sixty to one hundred dolphins, feeding in and out of the surf, progresses rapidly along the coast with no distinct or permanent subgrouping; accurate counts of individuals in such schools were not possible. Dolphins sometimes formed up temporarily abreast to follow a swell, simultaneously disengaging as it broke.

“groups” within which there were further independent stable divisions of two to ten individuals termed “subgroups”, is illustrated in Fig. 2. Tail slapping, chasing and biting behaviour—frequently associated with sexual and dominance disputes—was conspicuous in one disorderly group of twenty individuals. Another group of ten, swimming in close proximity in line-astern formation, had no distinct subgroups. Lone dolphins were scattered on the periphery of the school and between groups. This type of school was seen slowly progressing in the early afternoon when dolphin groups were normally engaged in play or sexual activity. Formations of this kind were rarely sighted from coastal vantage points; the more frequently seen progression was a scattering of dolphins with no very clear organization except for occasional subgroups (Fig. 3). Further examples of schooling formation, also seen infrequently from the coast, are shown in Fig. 4: the horseshoe formation (Fig. 4A) was associated with fish herding in deeper waters (20 metres) whereas the assembly of subgroups (Fig. 4B) was seen in schools proceeding rapidly close to the coast in deep water. Dolphin formations seen most commonly from the coast were either the isolated group (Fig. 4C) or subgroup (Fig. 4D).

Subgroups in free-ranging and captive dolphins varied both in numerical composition and in spatial deployment. Frontal, dorsal and lateral views for a trio of dolphins are shown in Fig. 5. It was not always clear whether specific formations were related to definite functions but the following observations provided a clue to the nature of some of the patterns of deploy-

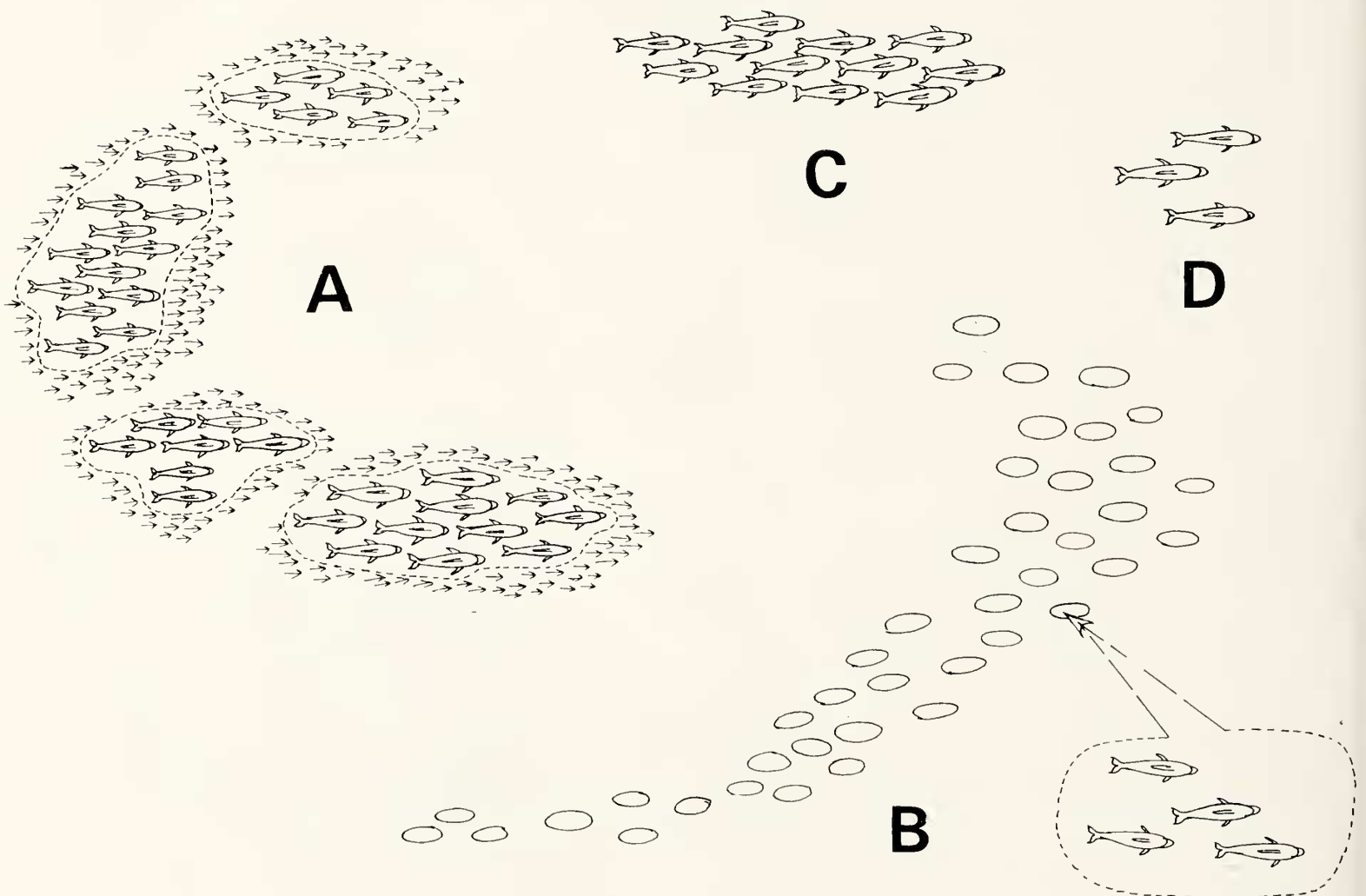


Fig. 4. Schooling, grouping and subgrouping in bottlenose dolphins. A. A horseshoe formation of four groups without distinct subgroups. B. A wing formation of subgroups only. C. A group—more than six dolphins—without subgrouping. D. A subgroup.

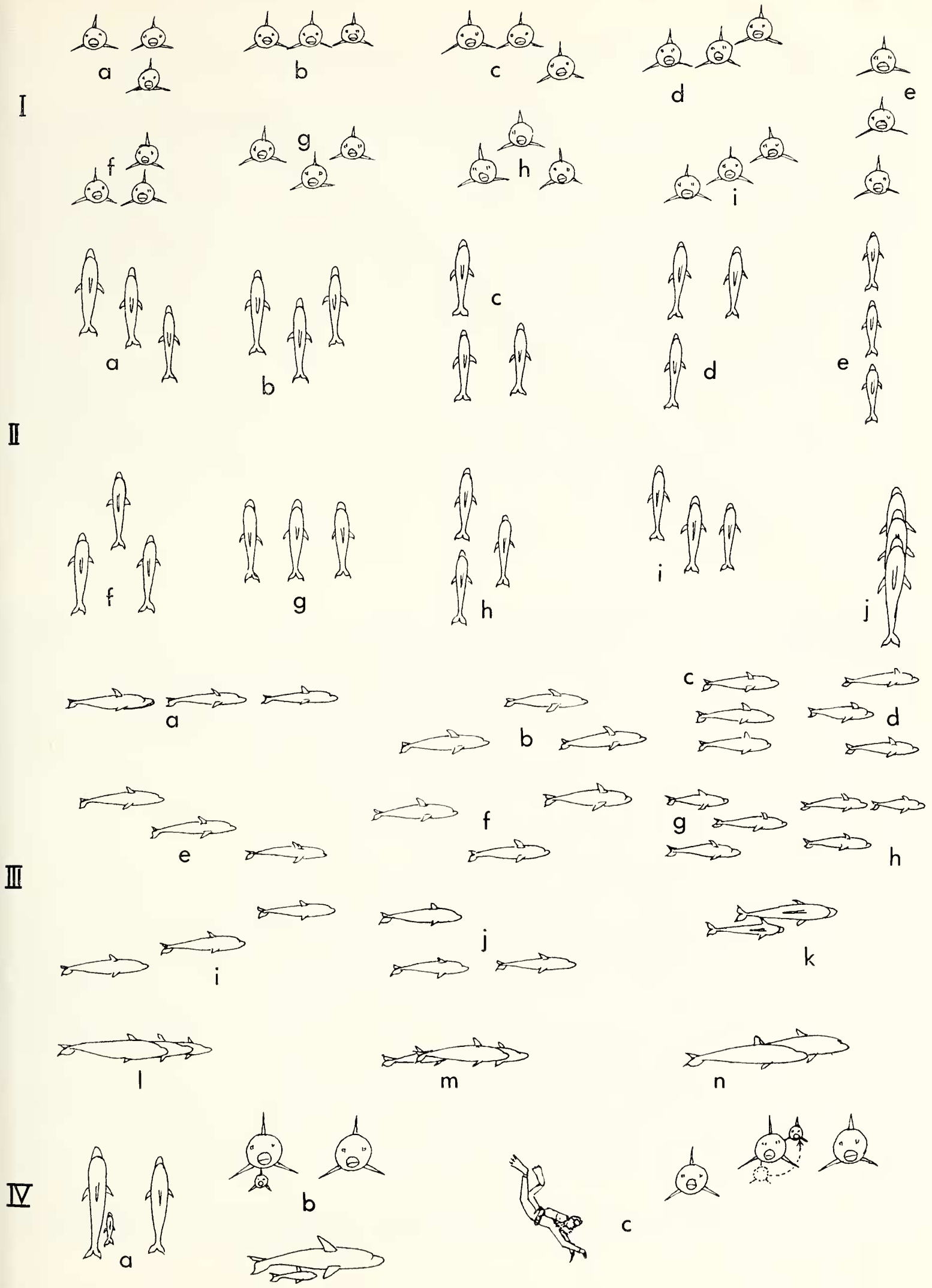


Fig. 5. I, II and III. Frontal, dorsal and lateral views of variations in spatial deployment of bottlenose dolphins. For convenience, only a trio is illustrated. IVa and b. Positions adopted by a young calf. IVc. Change in position of calf in uncertain situations.

ment: the spearhead was commonly seen when dolphins investigated a source of alarm near the surface (Fig. 5, I_h, II_f), or near the bottom (Fig. 5 I_g, II_f) of the pool. In both cases the leader, the dominant dolphin, was deployed on the vertical plane closest to the alarm. Similarly, the presence of a diver in the tank stimulated a change in the position of the calf from beneath the belly of her mother to her far side (Fig. 5 IV_c). A functional formation, seen only in cows, was the linking of two individuals by the extended flipper of an apparently dozing cow which maintained contact with the abdomen or flank of the leading, vigilant animal (Fig. 5 III_k, III_n). The close co-ordination was remarkable as the dolphins progressed, disengaging contact momentarily while surfacing for air, apparently communicating throughout by tactile stimuli. Indeed, the importance of tactile stimuli in establishing and maintaining mother-calf formations was clearly evident from birth.

In free-ranging dolphins comparable re-arrangements of formation occurred but in the majority of cases the causes were not discernible. Inspection of Fig. 5 demonstrates that many combinations were possible when sex, age class, number of individuals and circumstances varied. Inter-specific encounters influenced group progressions, subgrouping and formations. Two examples of co-ordinated avoidance responses to potentially dangerous hammerhead sharks (*Sphyrna zygaena*) and a lone blue pointer (*Carcharodon carcharias*) are illustrated in Fig. 6. As the dolphin group divided to skirt the hammerhead sharks, a subgroup of two

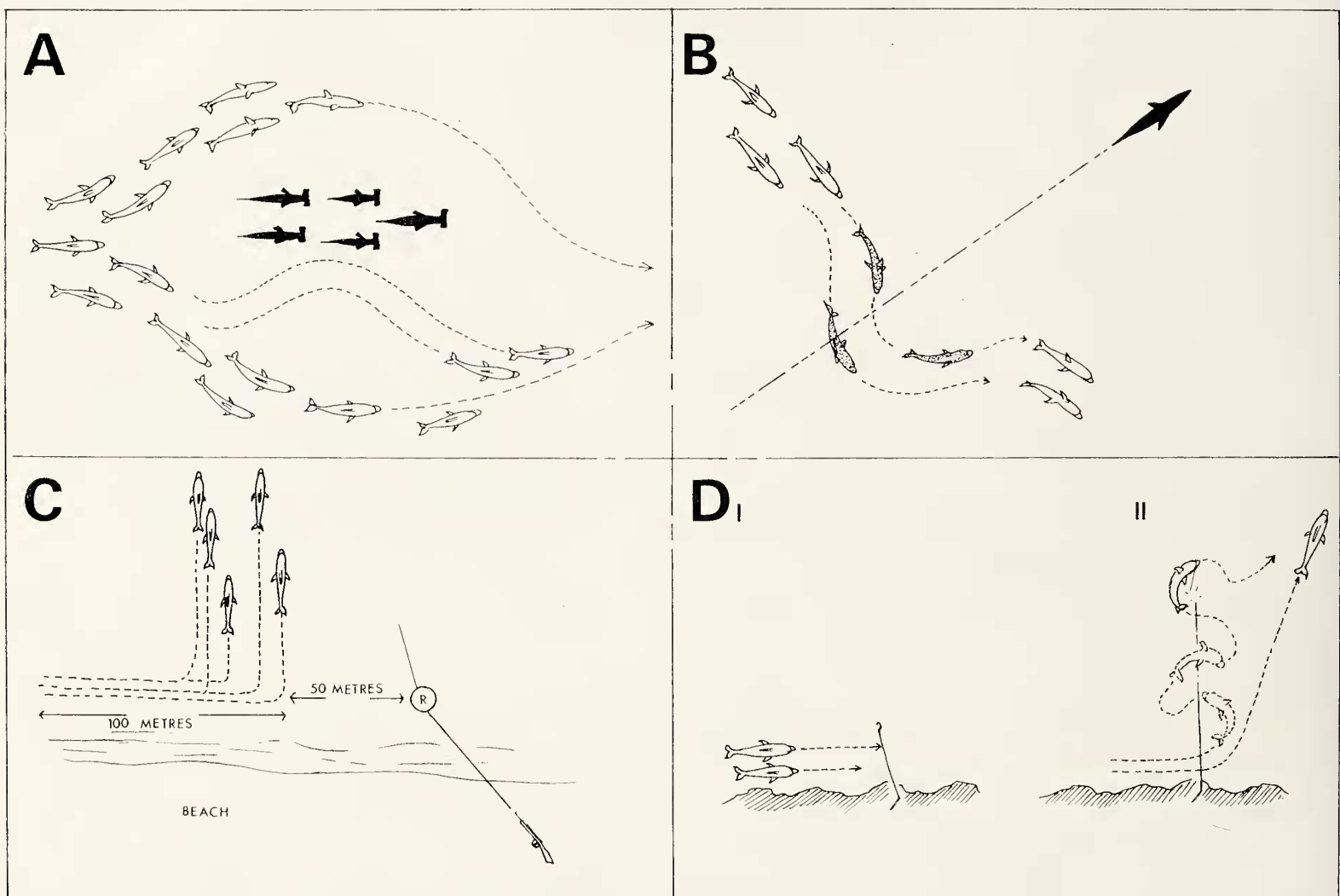


Fig. 6. Avoidance responses by bottlenose dolphins. A. and B. Co-ordinated avoidance of hammerhead and blue pointer sharks. C. and D. Unco-ordinated presipitate flight in response to unusual and alarming stimuli.

individuals formed on one flank, increased speed and passed at close range; the group reformed with the sharks in its wake (Fig. 6A). The dolphins gave the larger, more formidable blue pointer shark a wider berth by sounding to a depth greater than ten metres (Fig. 6B). Shark attacks on dolphins are known to occur (Lineaweaver, 1967) but the incidence, severity or cause of the attacks have not been fully evaluated. It is possible that the exploratory approaches of the younger animals and the policing manoeuvres of the dominant dolphins provoked retaliatory or predatory responses by sharks. It was perhaps of significance that Dolfie, considered to be a dominant bull of a free-ranging group, bore the scars of a recent shark bite (Plate 16) and that an attack on an apparently immature male dolphin (*Tursiops truncatus*) has been reported (Caldwell, Caldwell and Siebenaler, 1965). Encounters with killer whales (*Orcinus orca*), probably the only true predator of dolphins, were never witnessed in detail. Tape recordings of killer whale sounds played to our captive dolphins stimulated rapid swimming, tight formations and fear responses whereas recordings of other marine species did not have these effects.

Subgroups of dolphins of unknown age or sex classes made exploratory approaches to Cape fur seals (*Arctocephalus pusillus*) sleeping on the surface. In captivity Haig played extensively with Tommy, a young bull seal (Plates 17 and 18). This play activity, which had no aggressive overtones, developed after several years into obvious sexual approaches by both animals and culminated in attempted copulation. It was initiated when exploratory burst of high speed swimming close to the sleeping seal developed gradually into games of chase.



Plate 16. Dolfie, an adult bull, was captured from a free-ranging group bearing the scars of a recent shark bite in the motor muscles below the dorsal fin. Note the extensive "raking" by the teeth of other dolphins.



Plate 17. Haig, playing with Tommy, a subadult Cape Fur Seal.

In marked contrast to the orderly formation maintained by dolphins in the vicinity of sharks, precipitate flight was shown by a group when a shot from a light calibre rifle was fired into the water fifty metres ahead of an approaching group swimming parallel to the shore: all animals turned simultaneously for the open sea and fled with the distance separating them increasing in the line of flight as the fastest dolphins outpaced the others (Fig. 6C). In another incident, when one of a subgroup of two individuals was inadvertently foul-hooked on light fishing tackle, both turned for the open sea but the hooked animal was left far behind leaping high into the air to free the line which had already parted (Fig. 6D). In both of these encounters with extraordinary and alarming stimuli, therefore, the organized and co-ordinated mode of progression had broken down.

The availability of favoured food fish (shad—*Pomatomus saltator*) partially determined the pattern of movement of bottlenose dolphins along the coast in the early morning and in the late afternoon, at which times feeding activity was most prominent; the capture of squid, a known dietary component of dolphins was never witnessed. Due to the popularity of shad angling, it was well known that this species of fish frequented certain feeding places, mainly in turbulent water just beyond breaking surf and rocky outcrops. It was often noticeable that shad came on the bite when bottlenose dolphins appeared two to five hundred metres distant.



Plate 18. Tommy, hanging limp, permitted Haig to gently grasp and tow him during extensive periods of play.

Dolphins progressed in scattered groups, sometimes spread out about 800 metres in length along the coast. Group cohesion was not a marked feature of such groups and dolphins captured fish on an individual basis. However, some splashing seawards of the surf by animals leaping clear of the water with body bent concave downward and landing on their sides with a resounding report was generally present; although this behaviour in captive animals was associated with the later stages of pregnancy and in known cases of gastronomic discomfort, it was thought, because of the orderly fashion in which the leaping was effected by several animals in line-astern formation, that this procedure in the present instance related to fish herding. In contrast, organized herding by bottlenose dolphins of shoals of fish was seen, both in the open sea and at the confluence of rocks and beach. An incident, observed in clear water from a vantage point on Robbeberg at Plettenberg Bay, is illustrated in Fig. 7. A group of dolphins was sighted containing a shoal of shad at the intersection of a rocky promontory and a sandy beach. A large dolphin (A), judged by overall size, shape of head and dorsal fin, to be a bull, circled a prominent route equidistant between rocks and surf: lactating cows, entering the surf to feed, left their calves in the company of other cows in the close vicinity of this animal. Dolphins fed from the periphery of the shoal along the escape routes of the fish but at no time attempted to feed directly into the trapped main shoal which would probably have been dispersed. Dolphins continually arrived from and departed to the open sea, but at all times there were sufficient numbers to keep the fish tightly herded. A second large dolphin (B), also thought to be a bull, appeared from time to time in the position indicated in Fig. 7; the impression was gained that this dolphin patrolled a route to and from the open sea as

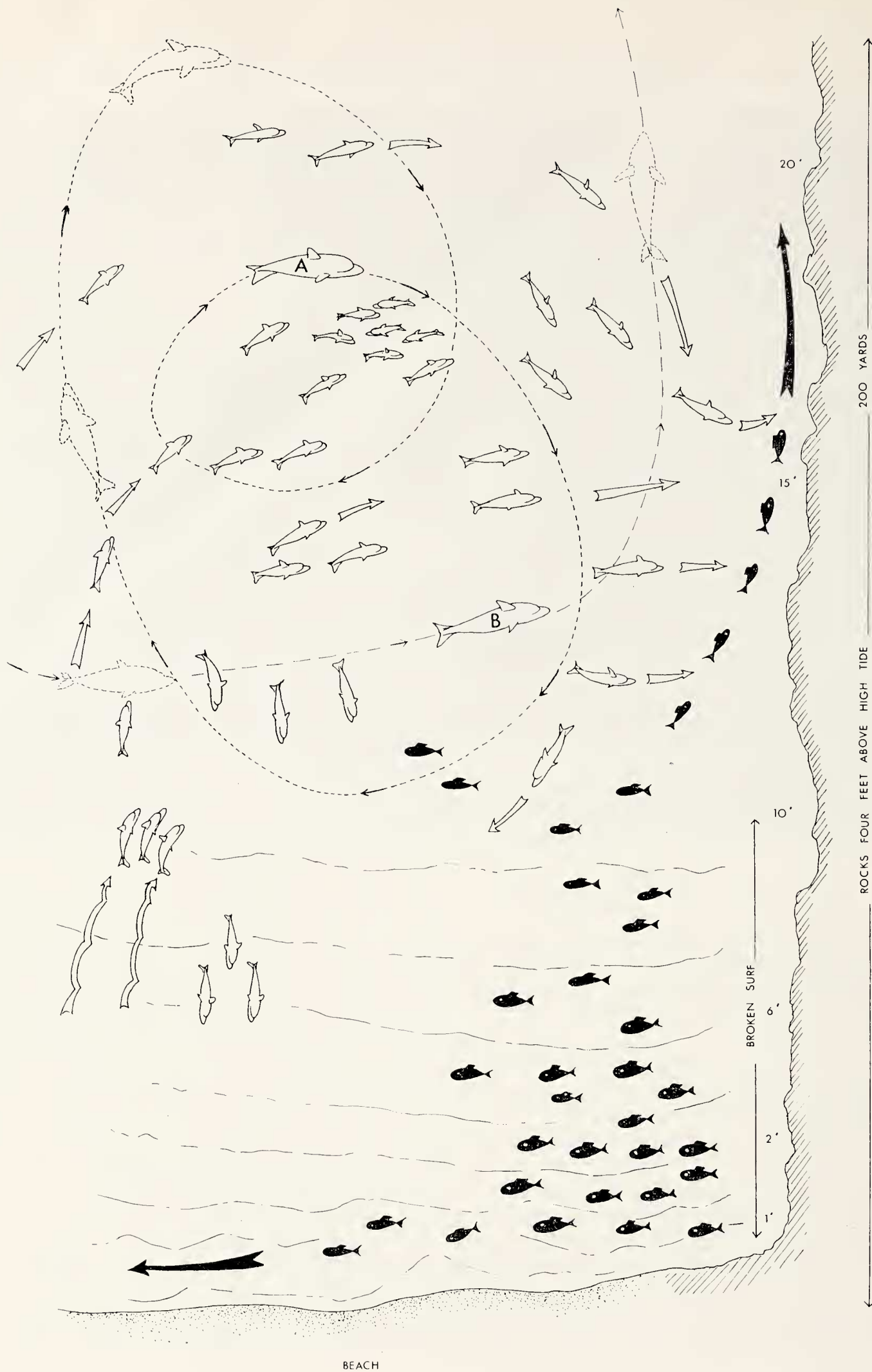


Fig. 7 Organized herding, retention and capture by bottlenose dolphins of a shoal of shad.

indicated by the dotted line. The routes followed by dolphins A and B, the fact that they returned to specific areas after intermittently capturing a fish, as well as their apparent control over the central area in the proximity of the immature dolphins, gave the strong impression that they were performing a supervisory function over what appeared to be a highly organized herding and capturing manouevre.

A similar incident was witnessed from its inception in the open sea. Bottlenose dolphins, leaping and splashing as described above, converged slowly from opposing flanks and gradually a tightly packed shoal of fish became discernible as a dark-coloured mass beneath the surface between the encircling dolphins. Simultaneously, dolphins could be seen darting under the shoal and thus preventing it from sounding. The shoal was consumed from the sides and underneath while the whole ensemble progressed slowly out of sight at about 7 k.p.h. These observations suggested that the two distinct types of feeding activity seen in bottlenose dolphins were part of the same process: the scattered groups of feeding dolphins, extending over long stretches of coast generally contained some leaping and splashing individuals, and these activities might well have driven fish ahead until they were herded into a suitable position where they could be contained and captured from the periphery as in the above examples.

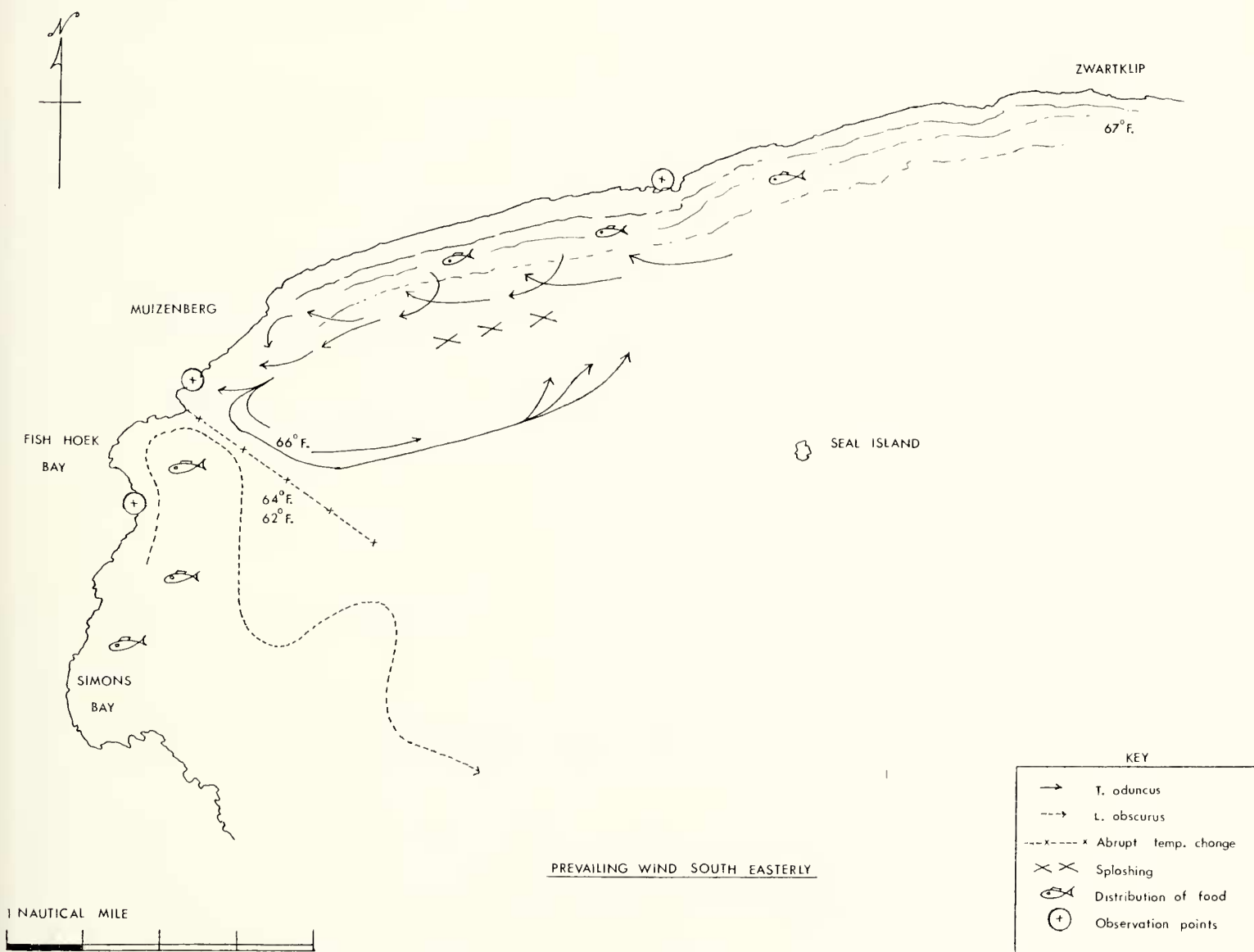


Fig. 8. The influence of water temperature upon the day ranging of two delphinid species.

A school of dusky dolphins (*Lagenorhynchus obscurus*) was observed feeding at Hout Bay in the Cape. A single dolphin found a shoal of pilchards (*Sardinops ocellata*) stationed behind an outcrop of rocks in deep calm water. As the dolphin turned towards the pilchards, the school of approximately two hundred dolphins, scattered over an area of about eight square kilometres, immediately converged on the area and commenced feeding. This suggested that the presence of the fish had been communicated to the other dolphins. Experiments at the Oceanarium have shown that all of the dolphins are aware of the information reflected when sonar is employed by any one dolphin, and thus no intentional transfer of information need be posited as an explanation of this incident.

The feeding pattern of humpback dolphins (*Sotalia lentiginosa*) differed markedly from that of bottlenose and dusky dolphins: humpbacks were comparatively slow-moving animals, generally seen in compact groups ranging in number between three and twenty individuals. They seldom leaped out of the water, and when this happened it appeared to be associated with courtship in adults, or play in juveniles. In areas where the sea bed was sandy with outcrops of isolated reefs, humpbacks moved systematically from one outcrop to the next, feeding leisurely and remaining submerged for comparatively long periods. Groups, sometimes separated in time by several hours, usually inspected the same reefs, following similar routes and it was noticeable that they never entered the surf. A group sometimes divided into two or more subgroups at widely separated reefs but, because they later reunited, had apparently maintained acoustical contact. Lone individuals were also seen.

Water temperature appeared to limit the distribution of various species of dolphins. Seasonal fluctuations in warm and cold ocean currents were associated with mass movements of dolphins apparently over great distances. In addition, sudden changes in climatic conditions affecting water temperature influenced dolphin ranging within specific areas; the presence of dolphins in sheltered bays in spring often indicated an impending wind change. In captivity sudden fluctuations in both the atmospheric humidity and the water temperature of the pool strikingly influenced the temperament and appetite of the dolphins. Free-ranging bottlenose dolphins feeding on shad habitually followed certain routes; in the example shown in Fig. 8 they on occasions turned sharply from the normal route at the thermocline in spite of there being abundant shad beyond. The only detectable factor correlated with this deviation was the sudden fall in water temperature at this point. Similarly, dusky dolphins, normally frequenting colder waters, turned at the opposite side of this thermocline. Again, their known food fish (pilchards) were distributed throughout.

DISCUSSION

The primary purpose of this comparative review was to assess our current knowledge of the naturalistic behaviour and social organization of Indian Ocean dolphins. It is clear that, in contrast to the more easily accessible and identifiable terrestrial baboons, the study of ranging and migratory behaviour, group composition and population dynamics of free-ranging dolphins is greatly handicapped by the lack of suitable marking techniques. A further limitation is our incomplete understanding of the acoustical perceptual systems employed by cetaceans.

A useful feature for day to day identification, apart from differences in physical size of individual dolphins, is the pattern of atrophying skin on the posterior edge of the dorsal fin in association with the characteristic inclination of the fin in certain individuals; notches in the anterior peduncle occur less frequently and are less conspicuous. Such natural markings are of short-term value only, since in two captive animals these features underwent many changes in seven years. Similarly, deep scars lose their prominence and continuous skin replacement in dolphins (an algae growth-inhibiting mechanism) appears, therefore, to militate

against branding as a marking technique. Tagging was considered in 1962, but experience with reactions to physical marking or tagging was necessary. Violent physiological rejection of foreign bodies occurs: fish spines piercing the blubber become rapidly encapsulated and large subcutaneous abscesses erupt after several weeks with gross tissue damage. It is likely that rapid repair to damaged surface tissue is an adaptation in these deep-diving marine mammals, with consequent slow replacement of underlying tissue, from beneath, resulting ultimately in the rejection of the foreign body together with the entire surrounding affected area. Placing either loose or tight-fitting loops as markers around the peduncle are likely to injure the animal, since captive dolphins exhibit abrasions as the result of exerting mild pressure on a towing loop for only four minutes each day; apart from streamline-spoiling in these fast swimming animals, bottlenose dolphins show great stress in response to the attachment of any device, however small. A large number of unsuccessful tagging experiments on four species of dolphins have been conducted in Japan (Nishiwaki, Nakajima and Tobayama, 1966). The identification of animals inhabiting an aquatic three-dimensional environment is limited by conditions of water clarity: dolphins, marked or unmarked, are partially visible only every ten to sixty seconds when they surface to breathe in the normally unstable surface plane. Apart from the prohibitive cost of a systematic tagging programme on our coast—assuming the development of a suitable marker—the problems are even further compounded by the nomadic nature of the dolphin and by its reluctance to return to areas where it has previously been molested.

Underwater chambers have been used to observe cetaceans in their own element (Evans and Bastian, 1969). However, unfamiliar objects are likely to stimulate apprehension and to restrict behaviour: observation of dolphins in clear water from elevated coastal observation points has frequently shown that their behaviour is markedly influenced by the approach of a skin diver or boat. Groups of bottlenose dolphins often deploy on a vertical plane (Fig. 5 Ie) in order to obtain a clearer view when investigating a skin diver underwater: Tayler and others have on occasion been threatened with open mouth by large individuals while swimming amongst free-ranging dolphins. On the other hand, underwater devices, although provoking caution, may hold groups of dolphins fascinated for considerable periods but only within the inevitably limited range of view: multiple underwater television devices would suffer, to a lesser extent, from the same limitations and also from inherent sound propagation. Until technology has evolved a suitable vehicle for keeping pace continuously with known groups of dolphins, so that the animals become habituated to a neutral observer, as occurs in groups of non-human primates (see under "The Animals," p. xx), the most rewarding compromise appears to be to observe undetected from high vantage points overlooking the sea.

Extensive work on dolphin phonation over seven years has revealed that the basic frequency sweep of the communicating whistle of an individual dolphin remains characteristic of that animal (Tietz and Tayler, 1964). Further, the whistle of the recently acquired bull Daan has also retained an individualistic frequency/time curve; when phonation commenced, Dolly likewise developed and retained this identifiable characteristic. This relationship probably remains reasonably constant for the lifespan of the dolphin. Similar constant relationships have been reported in *Tursiops truncatus* (Caldwell and Caldwell, 1965; 1968b) and were evident in the phonation of humpback dolphins at the Port Elizabeth Oceanarium. We are examining the possibility of applying these findings to determine the ranging and distribution of individual groups of dolphins by recording phonation in free-ranging animals from a motor launch. This method of recording is unsatisfactory: apart from the limitations set by the sea conditions, the dolphins are alerted by the presence of the boat and phonate infrequently, if at all, as is the case in alarmed captive animals. We intend to develop this line of investigation to a transportable system, incorporating waterborne transmitters, inconspicuously sited where possible, at strategic coastal observation points to record or relay

data to a receiving station in the acoustic laboratory in the Oceanarium where the data would be processed, ideally by computer. A closer investigation of the components of dolphin sonar may reveal similar individual characteristics. Should this method of acoustical identification of individual dolphins prove successful—and sound transmission in water is not limited by poor water clarity and nocturnal conditions—it should in addition prove possible to correlate phonation of free-ranging dolphins with that known to occur in experimentally controlled nocturnal and diurnal situations in captivity.

In drawing comparisons between animals differing as greatly in physiological and anatomical structure as do cetaceans and primates, it is as well not to lose sight of the substantial behavioural differences occurring between species even within the same genus. Attention has been focussed in this report upon a number of similarities between baboons and dolphins, but it is not intended to imply that the few, although important, common factors mentioned place them on a definitive behavioural plane. Indeed, if comparisons between non-human primates and dolphins are to be drawn, it is possible that the social organization of bottlenose dolphins will ultimately be shown to have more in common with that described for the more highly evolved chimpanzee (Goodall, 1965). Nevertheless, this review has indicated that the social organization of bottlenose dolphins and baboons are comparable with regard to: dominance hierarchies with co-operative functional behaviours of dominant males co-ordinating group activities; a mating system of rotating consort relationships without permanent sexual pair bonds; a slow maturation process with strong and extended mother-infant ties; close affiliative ties between females and infants other than their own offspring; highly developed investigatory and exploratory tendencies; play behaviour at times utilizing inanimate objects; play behaviour directed towards other species—for dolphins see Plates 17 and 18 and under "The Animals". p. 00 in this report and Alpers (1963, pp. 206—21)—for baboons see Plates 12 and 13 in this report and Goodall (1965, p. 436); evidence of functional deployment group co-ordinated responses to potential and natural predators.

It may be surprising that two forms whose terrestrial links date back 65 million years should have evolved independently, yet share these important behavioural features. A significant deviation from similar evolutionary behavioural patterns is the perhaps inevitable acoustical adaptation by cetaceans to their aquatic environment. The velocity of sound in water is some four times that in air with a corresponding fourfold increase in wavelength; the cetacean auditory system has therefore adapted to higher frequencies where wavelengths are comparable to those evident in the phonation of almost all terrestrial forms. It is remarkable that our dolphins have not learned to receive or to repeat—and the latter is possible by means of their sonar system, there being no vocal chords—the complex harmonic composition of human speech despite the very close human contact and frequent presentation of selected English and Afrikaans words played repetitively to the animals both in and out of water over many years. Hence, we postulate (in preparation) that the cetacean auditory system has developed without good frequency discrimination and consequently with poor tone perception—not characteristic of most terrestrial forms—but has developed great sensitivity to, and fine discrimination of, relative sound intensities in contrast to, for example, the more logarithmic response of the human auditory system to sound intensity. The sophisticated system of dolphin echolocation must depend largely upon exceptional perception of relative sound levels, the perception of very small time separations in pulsed sounds—as does electronic sonar—and an extremely low threshold of hearing, as yet not measurable. The small delphinid cochlea has relatively few turns, but a very wide frequency response: 100 herz (hz) to 110 kilohertz (khz) (Tietz and Tayler, 1964). This suggests either that only poor frequency discrimination can occur across such a wide frequency spectrum, or that fine frequency discrimination occurs only over a small part of it. Whereas terrestrial animals rely almost entirely upon generated sounds,

reflected sound is apparently central to acoustical perception in dolphins. Since echolocation, rather than vision, has been emphasized by evolutionary processes in dolphins it would be logical to assume that acoustical communication would develop in association *with the properties of reflected sound as in echolocation*. By this reasoning, terrestrial communication would, in contrast, develop on *an onomatopoeic basis*. Indeed, we are fully aware of the latter in teaching our offspring to speak. These considerations reinforce the interpretation (Tietz and Tayler, 1964) that amplitude modulation of a simple frequency sweep within 2 khz to 14 khz is the means of acoustical communication in bottlenose dolphins. Further, there is evidence to show that the form of some of these dolphins whistle modulations can be correlated with dolphin sonar echoes associated with specific objects, but in "summary" presentation. Some of our observations suggest that the communicating whistle is produced by the two independent nasal systems functioning simultaneously in phase-locked mode, and that modulation is effected by phase changes in the sounds emanating from the large, more central right-hand system—considered to be responsible for sonar generation (Tietz and Tayler, 1964)—in relation to the smaller left-hand system. The resulting modulation in phase changes from 0° to 180° may give rise to the typical wave envelope resembling that of an electronic balanced modulator. Our dolphins respond to human gestures within their limited visual range above the water, but the development of two-way communication is impaired by their anatomical structure. However, abnormal fluke, flipper and head movements made at appropriate times imply attempts at communication. It is significant in this connection that a chimpanzee had learned to employ American Sign Language to communicate more than thirty signs, although it has not been possible to develop vocal communication (English) in the same species (Gardner and Gardner, 1969). Acoustical communication in baboons may be divided into two categories employing a probable total of some twenty to thirty differently constituted sounds ranging from grunts to staccato barks. One category forms the means of long-range communication necessary for troop vigilance and cohesion (Stoltz and Saayman, 1970, pp. 130—131). The second category relates to the intergroup expression of aggression, fear, friendly and sexual behaviour. The system of dolphin communication, their sophisticated behavioural co-ordination and their extensive cortical development indicate that their level of social integration may well be far more complex than that found in the catarrhine monkeys.

The following projects for future research on dolphins are suggested by this comparative review:

1. Acoustical detection, identification and ranging studies of Indian Ocean dolphins.
2. Ecological studies of free-ranging dolphins.
3. Establishment of a larger group of captive dolphins containing representative age and sex classes in order to investigate more fully: dominance—with special reference to functional co-operation between bulls, the nature and influence of pair bonding upon intragroup relations, hormonal factors in reproduction, and the maturation and development of behaviour.
4. Continuation of the investigations of dolphin phonation, sensory perception and cognitive functions.

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